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IMPRIMÉ AU DANEMARK
ANDELSBOGTRYKKERIET I ODENSE

Bjørn Helland-Hansen
1877—1957

Professor Bjørn HELLAND-HANSEN passed away peacefully on 7. September 1957 at an age of nearly 80. His death means the loss of perhaps the last of the great pioneers of physical oceanography.

He was born in Kristiania (Oslo) and first studied law at the University. But soon he changed to medicine, and then, as he said, "I finally had the feeling of being really a student". At this time KR. BIRKELAND gave three lectures on the recently discovered X-rays. HELLAND-HANSEN attended these lectures, given by his former teacher,

and later assisted him at regular lectures. In 1898 he accompanied BIRKELAND as his assistant on the first Aurora Borealis Expedition from Tromsø into the desert regions of northernmost Norway. When in a snow-storm his fingers were frozen, he had to return and to give up medicine. Now taking up the study of natural sciences, he spent some time with Martin KNUDSEN in Copenhagen; that was his first contact with oceanography.

This happened at the century end, in those years of rapid growth of the study of the sea. In 1898 Vilhelm BJERKNES developed the circulation theorem. In 1900 Fridtjof NANSEN started the practical investigations of the Norwegian Sea — with HELLAND-HANSEN as his assistant. In 1902 two international organizations were established: the International Council for the Exploration of the Sea and the International Central Laboratory at Kristiania (Oslo), the latter under the conduct of NANSEN and with V. W. EKMAN as an assistant. This same year EKMAN published his theory on wind-driven ocean currents, and in the following years HELLAND-HANSEN applied the circulation theorem to the movements in the sea; through the formula for dynamical computations his name is for ever attached to the history of physical oceanography.

At this stage the need for practical observations of the highest possible degree of accuracy was realized. Instruments and methods had to be considered carefully. At the International Courses of Marine Research in Bergen 1902–1914 HELLAND-HANSEN was responsible for physical oceanography. In 1909 he completed, together with NANSEN, a thorough study of the data they had collected, the classical monograph "The Norwegian Sea".

As Director of the Biological Station, Bergens Museum, from 1906, HELLAND-HANSEN strongly felt the need of a research vessel, and in 1913 the "Armauer Hansen" was launched. This small vessel, only 76 feet long, was designed according to his own ideas; and on cruises in the North Atlantic, in the Mediterranean, in the Norwegian Sea and even north of Spitsbergen, she proved that these ideas were right. She served her purpose until last summer, when she was replaced by another, carrying HELLAND-HANSEN's name.

On his proposal Bergens Museum established in 1917 the Geophysical Institute, with one chair in hydrography, one in dynamical meteorology (Vilhelm BJERKNES) and, from 1928, one in geomagnetism and cosmical physics. Much due to HELLAND-HANSEN's initiative the Norwegian Geophysical Commission and the Norwegian Geophysical Association were established in 1917. And in 1928 he had the great satisfaction of seeing his institute in its own new building, a gift from citizens of Bergen.

His collaboration with NANSEN, and their intimate friendship, continued to the last. Among the several papers which they published together, the great treatise on "Temperaturschwankungen des

Nordatlantischen Ozeans und in der Atmosphäre" appeared in 1917, and "The Eastern North Atlantic" in 1927; in his paper "The Sognefjord Section" of 1934 HELLAND-HANSEN refers to ideas suggested by NANSEN immediately before his death.

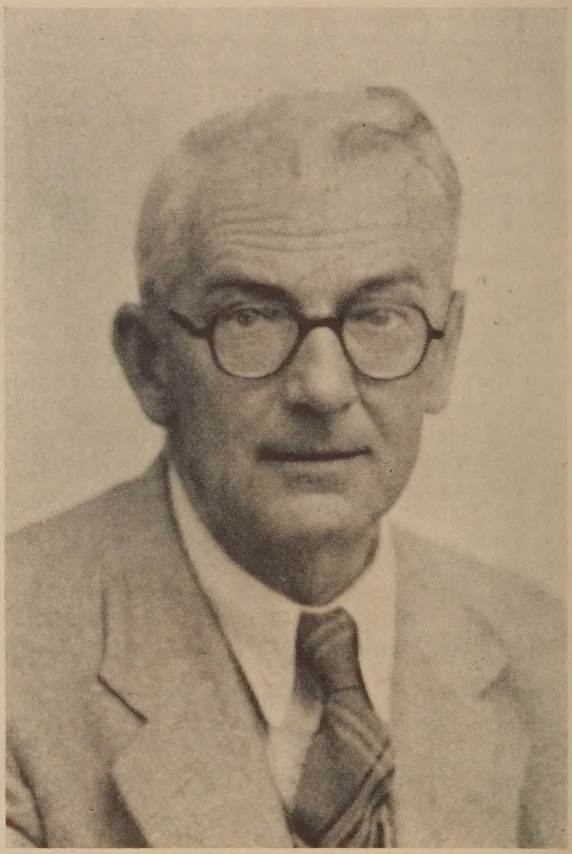
He co-operated with EKMAN from the early years, but particularly in connexion with experiments on current measuring from an anchored ship. They both participated in cruises with the "Armauer Hansen" in the Norwegian Sea in 1923 and 1924, and in the area between the Canary Islands, Madeira, Gibraltar, and Portugal in 1930. The results from the latter expedition were published by EKMAN shortly before his death.

In the early years HELLAND-HANSEN was interested in different branches of the study of the sea, and several of his papers are concerned with biological and fishery problems. But his main interest was directed toward the physics of the sea, but within international aircles he was less active in the International Council than in the International Union for Geodesy and Geophysics, where he had many commissions, among them those as President of the Association of Physical Oceanography and of the Union.

When in 1930 the Chr. Michelsen Institute was established at Bergen, the plans had been carefully prepared by CHR. MICHELSEN in intimate collaboration with HELLAND-HANSEN, who was also the director of the institute until 1955. The broad scope of interests of this institute "of Science and Intellectual Freedom" appealed strongly to the HELLAND-HANSEN of later years and gradually took most of his time.

This humanly very natural development and expansion of interests, together with his gentle way of negotiation and his extraordinary personal charm, also resulted in HELLAND-HANSEN being charged with many tasks of social intellectual life. For his scientific achievements he received a great number of titles, medals, and other signs of high appreciation. In oceanography his death marks the end of the pioneer period and will be felt with sadness throughout the world. But within many other branches of intellectual life it will be felt as the loss of one of the great personalities so rarely appearing among men of to-day.

Håkon Mosby



Robert Edward Savage

1887—1957

SOME men leave an impression on their colleagues by forceful leadership, burning zeal, or other not necessarily engaging positive characteristics, others who might at first sight be thought somewhat negative in their approach, influence their fellows by the quiet penetration of their example. R. E. SAVAGE who died on 20. October 1957 at Deganwy was of this latter type. In the varying circumstances of his life he maintained a patient dignity and an

unwavering allegiance to the high standards of integrity that he set himself in his scientific work. This attitude made itself felt on all his colleagues and in particular on the writer of these lines who counts himself fortunate to have served as his assistant in the plankton work carried out at the Lowestoft Laboratory during the period between the two world wars.

SAVAGE was born in 1887 at Leigh, Lancashire and spent his childhood in Burnley where he went to school and to the local Technical College before going to the Imperial College of Science in 1909.

The letters A.R.C.S. and D.I.C. which he obtained here are becoming less familiar today, so that it has to be remembered that when they were granted they conferred on the recipient the same cachet as a university degree. The zoology which he took as his special subject came to him through the distinguished and colourful exposition of Professor MACBRIDE. On leaving the Imperial College of Science in 1913 he was appointed to the Board of Agriculture and Fisheries where he worked as a young biologist in a small laboratory at 43, Parliament Street. His first fishery experience was concerned with the reading of herring scales. As a consequence he published a paper on the results, together with details of a method of determining rings by the use of polarized light which was both imaginative and sound.

In 1916, after a short course in bacteriology, he was seconded to the War Office as a civilian bacteriologist and was employed on the identification of amoebic dysentery at the General Military Hospital in Alexandria. He remained here until 1919 and spent the last year of this time as a lieutenant in the R.A.M.C.

The latter part of 1919 saw his return from Egypt to rejoin his department now re-named the Ministry of Agriculture and Fisheries. A new laboratory was acquired on the Marine Parade at Lowestoft and here his first work was the enumeration of North Sea plankton connected with a plaice spawning ground and the North Sea herring fishery. This type of investigation was to occupy most of his time between the two world wars, but in 1923 and 1924 he enjoyed a short interlude in which he made a study of the food of the oyster. The work was carried out at Orford in Essex from March 1923 to April 1924 and resulted in a most rewarding report. In this his mastery of technique is made abundantly clear to the reader and not least in the ingenious apparatus he devised to collect the gut contents of individual oysters.

From 1924 until 1938 he was occupied mainly with the plankton of the east coast of England herring grounds and with appraisals of the food of the herring. In the earlier part of the period, first with Sir Alister HARDY and later with the writer he published Parts I and II of a series called "Phytoplankton and the Herring" in which the occurrence of patches of phytoplankton was related to the distribution

of the herring shoals off East Anglia. Although a causal relation between phytoplankton patches and herring shoals was then a more strongly held hypothesis than it is today, it has to be pointed out that, with the evidence considered in retrospect, probably the best case of the interference of a fishery by a phytoplankton patch is that given by SAVAGE in a paper on the occurrence of *Phaeocystis poucheti*.

In July 1938 he was put in charge of the Ministry's shellfish laboratory and mussel cleansing station at Conway where he remained until he retired in 1954. Before this latter date his responsibilities had been increased by the addition of a sub-station at Burnham-on-Crouch. He proved a quiet, strong, and wise Director, so that, when, after his retirement, his services were recognized by the award of an O.B.E., all his friends and colleagues felt that the honour was a very appropriate one. While he was at Conway administrative duties put an end to his personal research work, but after he left he produced a paper on the great mussel spatfall at Conway in 1940 which was not only an important contribution on the effect of strong year groups on the rest of the population of a marine organism, but also proved that his hand had lost nothing of its old cunning.

Modern plankton work is rightly concerned in the dynamic appraisals for which the time is now ripe, but those who are engaged in this new direction would, I think, be the first to remember that their operations are only possible as a result of descriptive work and the patient enumerations by plankton ecologists of an earlier generation of whom R. E. SAVAGE was a shining example.

R. S. Wimpenny

Cube Photometer Measurements of the Angular Distribution of Submarine Daylight and the Total Submarine Illumination

By

W. R. G. Atkins and **H. H. Poole**

Introduction

In order to study the variation with depth of the average angle of obliquity (angle with the vertical) of submarine daylight we constructed a cubical photometer with six plane windows, and made measurements with it during 1938 and 1939, published 1940. These showed no significant change in the average obliquity with depth in the open sea, thus contrasting with the results of JOHNSON (JERLOV) and LILJEQUIST (1938) who worked in the Gullmar Fjord and at stations in the Baltic. Their results and ours afforded information on a matter of much botanical interest, the assessment of the total submarine illumination as received from all angles at a point. To determine this in air we had previously (ATKINS and POOLE, 1936) used an integrating sphere with internal diffusing surfaces mounted over a photocell. This was tested and shown to be independent, in its response, of the altitude and azimuth of the incident beam. As there are mechanical difficulties in the use of such an apparatus in rough weather it seemed preferable to ascertain the total illumination by calculation as described later. We attribute some differences between our results and those found in the carefully planned experiments of JOHNSON (JERLOV) and LILJEQUIST to the difference in the conditions, since ours were in the open sea exposed to the Atlantic swell.

The work of BIRGE and JUDAY in the Wisconsin lakes was continued by WHITNEY (1938, a, b, c) and DAVIS (1941), whose measurements were in many ways in accord with our own. WHITNEY, however, made calculations of the angle of incidence of sunlight with sky light of various proportions of relative intensity, and so arrived at effects of solar altitude upon the average angle of obliquity. In their calculations both he and DAVIS (1941) assumed spherical particles in suspension which scattered equally upwards and downwards, as LE GRAND (1939) did also. POOLE (1945) concluded that this assumption was not justified and our measurements of scattering (ATKINS and POOLE, 1952, 1954) showed that forward scattering predominated. Our work on the angle

of obliquity was confined to a study of the conditions which actually obtained in the English Channel, where the angle of incidence of sunlight (when present) is apt to show rapid variation. This somewhat obvious point has been stressed only because our unpublished results were criticized owing to their lack of agreement with some of Whitney's (1941 a, b) findings for lakes and sheltered coastal regions, but including one series of results just beyond the Continental Shelf at 71° W. longitude.

Our work was resumed after the war, colour filters other than green were also used. The more important results are given below.

The Cubical Photometer and Colour Filters

The cube had on each face a toughened plane glass window, outside which there was room for a colour filter under an opal diffusing glass mounted level with the rim of the metal ring surrounding the window. Close inside each window was a German "Electrocell", a selenium rectifier about 40 mm. diameter. The deck cell was an American Weston selenium cell similarly mounted and on gimbals. The submarine cells are connected by a seven-core insulated cable to a set of switches, so that any cell or combination of cells may be connected to the measuring apparatus. Currents were measured with our potentiometer telephone method with the Campbell-Freeth zero-resistance circuit, (Atkins and Poole, 1940; Poole, 1925; Poole and Atkins, 1929, 1934, 1937). In fairly steady light six measurements can be made in one minute, a speed not attainable with any marine galvanometer, and for long use less tiring.

The work done in 1938 and 1939 was resumed after the war, the cells having been re-calibrated in daylight, as described later. The corrections applied to the readings include (a) allowance for the different sensitivities of the six cells used in the cube and of the deck photometer; (b) allowance, if necessary, for any lack of linearity of the light current relation for each cell; (c) correction for the fact that owing to reflection effects the sensitivity of a submerged photometer is reduced; and (d) correction for the fact that, with the modified Campbell-Freeth zero-resistance circuit used to measure the currents, some current is taken from the potentiometer.

Of these corrections (a) and (b) are much the most troublesome, as all rectifier cells that we have tested lose some of their sensitivity with age. Moreover the "curvature" error increases, so that the fall in sensitivity for strong light may be much greater than that recorded with a test lamp. Good cells, when new, have a rectilinear portion of the curve which may for the 40 mm. size extend to 4·0 mA, but this decreases with age and is influenced by the moisture content of the air in the container. Some cells, especially after use, show curvature down to the smallest currents in microamperes. We accordingly made it a practice to mount the cells with dried silica gel, and to compare all successively with a vacuum emission cell, similarly mounted below a colour filter and surmounting opal. The exposures were made on the parapet of the laboratory roof on a day with bright and steady light, using galvanometers either on the roof or in a room below. By adding extra opal glasses with blackened rims underneath the usual opal, the illumination could be cut down to known fractions of the total. The transmission of each combination was found by

experiment and not by multiplying the factors of the individual opals. This is necessary on account of the reflections between the surfaces, and results in a transmission higher than that found by multiplication.

Correction (a) for the reduced sensitivity of a submerged photometer is allowed for by multiplying all submarine readings by 1·09 (Atkins and Poole, 1933) a factor which does not affect the ratio of the readings at different depths and is unimportant compared with errors due to drift and the shadow of the ship (Poole, 1936). Correction (d) for the circuit is in many cases under 1%, and, with our apparatus never exceeds 9%. It is read off from a graph (Poole and Atkins, 1934).

The arrival of a hired Admiralty-designed motor fishing vessel M.F.V. 1564 enabled us to start again, and series C12 (12. July 1946) and C13 were obtained 2 miles east of the Eddystone, also C14 at International Hydrographic Station England No. 1 (E1), 50°02′ N. lat. and 4°22′ W. long. about 10 nautical miles S.W. of the Eddystone. These series were carried out after the Electrocells and deck Weston had been carefully compared with an emission vacuum cell as described.

In view of a further probable alteration in sensitivity in these cells, which had been eight years in the cube, they were later replaced by newly-bought Evans cells, and the deck cell by a Megatron, but only after considerable delay owing to the damaged condition of the laboratory and to other work. The Evans cells were fitted into the cube, but in Electrocell holders as their own were too large. But one old Electrocell was used for the cube cell that faced downwards, U, as its characteristics were better than those of the sixth new cell. These new cells were highly sensitive, and gave rectilinear relations between current and intensity as follows:— for V, the cell facing upwards, to 4·36 mA, for the cells in four perpendicular azimuths A, B, C, and D, up to 1·40, 1·30, 1·00, and 1·60 mA, respectively, and for U up to 2·00 mA, all with VG 9 filters. The 20 mm. Megatron, with about one quarter of the area of the cube cells was rectilinear up to 1·00 mA. The new cells were used in the CN series of which CN20 and CN22 are given here.

Measurements at Sea

Tables 1 to 6 summarize the results obtained. In these m. is the depth below the surface in metres with b, just below; t the temperature in °C. as found with the standard Nansen-Pettersson bottle, and the vertical illumination recorded under the given light filter, is expressed as a percentage of that above the surface in a position as free from shading as possible. The light filters, BG 12, VG 9, etc., were the standard types made by Schott of Jena. Approximate limits for transmissions 50% of the maxima (as supplied by the maker) are given in Tables 2 and 6. In the tables μ_v is the vertical extinction coefficient for the depth interval immediately above the level opposite which it is printed. A/V, B/V, C/V, D/V, and U/V are the illuminations recorded by the four cells, A, B, C, and D, with vertical faces, and U facing downwards, expressed as percentages of the corresponding value of V, the vertical illumination recorded by the cell facing upwards.

We have already (Atkins and Poole, 1940) pointed out that H/V is approximately equal to $\pi\,(A + B + C + D)/4\,V$ where H is the horizontal component

Table 1

Series C12, 12. July 1946, noon to 13.15 GMT. Three km. east of the Eddystone. Depth 56 m. Clear sun, blue sky. Secchi disk 20 cm. diameter seen to 16 m. in shadow of ship, sea glassy, no wind

		Colour filter			
		BG 12 (blue)		VG 9 (green)	
Depth m.	t°C.	%	μ_v	%	μ_v
b	19·45	90	–	–	–
1	–	–	–	80	–
5	15·00	51	0·080	61·5	0·066
10	13·93	36·5	0·067	47	0·054
15	13·52	–	–	32·5	0·078
20	12·94	12	0·112	19	0·115
25	–	–	–	10	0·121
30	–	2·2	0·169	–	–
40	–	0·45	0·162	1·6	0·124
50	–	0·10	0·146	0·29	0·172

of the total illumination expressed as a percentage of V. Thus $H/100\ V$ is the mean tangent of the obliquity, and without serious error we may take $\theta = \tan^{-1}(H/100\ V)$ as the mean angle of obliquity. Values of θ are given in Tables 3, 4, and 5.

Results and their Discussion

Series C12 is shown in Table 1. The following points are of interest:—

(a) The warmer water above the 15 m. level was much clearer than that lower down. This is probably due to the fact that, as shown by Atkins and Jenkins (1953) and by Jenkins (1955), the sea at the end of June is at a summer minimum of phytoplankton and relatively unaffected by mineral matter in suspension owing to the calmer conditions. But when regeneration of phosphate occurs it appears first in the deeper layers in which the bright weather permits of the multiplication of the phytoplankton.

(b) Even in this water which was very clear down to 15 m. the extinction for blue light was considerably higher than for green.

Series C13 included measurements with a number of colour filters as summarized in Table 2. Earlier comparisons of colour extinction at the Eddystone position may be found in Poole and Atkins (1937), with Secchi disk visual range 16 m. on 21. September 1936. No definite temperature discontinuity is shown in Series 13, but a gradient from top to bottom. The decrease in μ_v for RG 1 and RG 5 is mainly due to the more rapid extinction of the longer wave-length they pass. Moreover the extinction is here mainly due to absorption, and we might expect the average obliquity to decrease with increase in depth.

In this water of moderate opacity μ_v was considerably larger for blue than for green; this is not only due to scattering but is probably influenced by the heavy chlorophyll absorption band with a maximum at 430 mμ. Red light was more rapidly extinguished, mainly due to absorption by water, but augmented by the chlorophyll band, very marked though less heavy than that in the blue, with a maximum at 665 mμ.

Table 2

Series C13, 26. August 1946, 10.30 to 14.55 GMT. Three km. east of Eddystone. Depth 56 m. Sun and blue sky, light clouds, rather variable, overcast later. Sea glassy, slight swell. Secchi disk visual range in shade 12·4 m., save for the VG 9 series the measurements were made using a Tinsley 10 ohm marine galvanometer

		Colour filter									
		BG 12		VG 9		VG 9 + OG 2		RG 1		RG 5	
Depth		340–480 mμ		480–580 mμ		550–580 mμ		> 600 mμ		> 675 mμ	
m.	t°C.	%	μ_V	%	μ_V	%	μ_V	%	μ_V	%	μ_V
1	15·35	77·5	–	94	–	71	–	58	–	36	–
5	15·24	43·5	0·143	–	–	34	0·185	10	0·436	2·15	0·70
10	14·70	18·1	0·176	31·5	0·121	16	0·150	1·6	0·375	0·102	0·52
15	14·32	–	–	18·0	0·111	6·7	0·173	0·21	0·399	–	–
20	14·21	2·19	0·211	10·0	0·119	2·5	0·197	0·047	0·302	–	–
25	–	–	–	4·4	0·164	1·15	0·155	0·008	0·349	–	–
30	14·10	0·27	0·210	2·55	0·109	0·51	0·164	–	–	–	–
40	–	0·047	0·175	–	–	–	–	–	–	–	–
50	13·95	0·010	0·156	–	–	–	–	–	–	–	–
Means											
1–20m.	–	–	0·187	–	0·118	–	0·176	–	0·380	–	–

Table 3

Series CN20, 8. July 1949, 11.20–13.35 GMT. International station E1. Depth 74 m. Hazy blue sky, cloudless. Wind east, force 2. Slight swell with ripples. Secchi disk 16 m. in sun, shade not possible. At 0.5 m. depth 16.47°C. All measurements with colour filter VG 9

Depth m.	t°C.	%	μ_V	A/V	B/V	C/V	D/V	U/V	H/V	θ
5	16·38	58	–	35.5	34·7	(56·0)	(53·2)	1·91	(141)	(55°)
10	16·22	40	0·074	37·4	18·2	7·0	12·4	2·05	59	30·5°
15	15·50	32	0·043	30·4	26·5	8·0	12·8	1·76	61	31·5°
20	15·42	16·5	0·134	31·0	29·4	11·2	12·0	1·51	65·5	33·5°
25	12·50	10·0	0·100	26·1	29·5	11·0	11·3	1·55	61	31·5°
35	12·40	3·75	0·098	32·0	22·2	15·4	15·4	1·69	67	34°
50	12·36	1·31	0·070	25·0	26·4	18·8	17·6	2·51	68·5	34·5°
60	–	0·625	0·074	24·3	23·2	12·2	13·6	–	57·5	30°
70	12·32	0·415	0·041	24·2	19·7	14·8	15·2	–	58	30°
Means		–	0·079	28·8	24·4	12·3	13·8	1·85	62	32°

Series CN20 and CN22, with the new cells are the most interesting of those obtained in 1949. The 5 m. values of C/V and D/V are extraordinarily high in Table 3 (CN20). With the slow drift of the ship to the west the vane attached to the corner of the cube between A and D should have kept A, B, C, and D facing approximately S.E., S.W., N.W., and N.E., respectively, thus accounting for the asymmetry of the deeper readings. It is possible that with the very light wind and slow drift the photometer may have rotated when first lowered. These values have accordingly been disregarded when taking averages.

Series CN20 (Table 3) and CN22 (Table 4) both show a reduction, with increase in depth, in the difference between the readings of the horizontal light

Table 4

Series CN22, 17. Aug. 1949, 11.50–14.05 GMT. Station E1. Depth 74.5 m. Clear blue sky, horizon whitish. Wind force 3, slight swell, a few waves breaking. Secchi disk in shade 18 m. All measurements with colour filter VG 9. Subsurface balance impossible. At 0·5 m. depth 16·00°C.

Depth m.	t°C.	%	μ_v	A/V	B/V	C/V	D/V	U/V	H/V	θ
5	16·00	62		4·3	12·0	43·5	13·7	1·69	57·7	30·0°
10	15·96	41·5	0·080	–	–	–	–	–	–	–
15	14·90	24	0·109	6·5	23·2	50	13·0	1·66	72·8	36·1°
20	13·88	12·2	0·135	–	–	–	–	–	–	–
25	13·80	6·5	0·126	9·4	19·2	49·5	16·8	1·65	74·6	36·7°
30	13·77	4·3	0·082	–	–	–	–	–	–	–
35	–	2·61	0·100	12·2	17·2	41·5	22·7	3·02	73·0	36·4°
40	13·77	1·70	0·100	–	–	–	–	–	–	–
45	–	0·94	0·118	12·0	19·7	50	29·5	–	85·0	40·4°
50	–	0·72	0·053	–	–	–	–	–	–	–
55	–	0·33	0·156	13·6	20·6	44	24·6	–	80·7	38·9°
60	–	0·25	0·055	–	–	–	–	–	–	–
65	–	0·16	0·091	14·3	18·7	21·7	18·7	–	57·6	29·9°
70	13·70	0·09	0·111	–	–	–	–	–	–	–
Means	–	–	0·101	10·3	18·7	42·9	19·9	2·00	71·7	35·5°

Table 5

Comparison of results (VG 9 filter)

Date	Series	Station	Depth m.	Sky	μ_v	U/V	θ
30. May 1939.....	C10	L 4	50	High sun	0·076	2·10	38°
8. July 1949.....	CN20	E 1	74	—	0·079	1·35	32°
17. Aug. 1949.....	CN22	E 1	74	—	0·101	2·00	35·5°
25. Oct. 1938.....	C3	L 5	56	Cloud 10	0·110	3·02	36°
26. Oct. 1938.....	C6	E 1	71	Low sun 24°	0·112	2·98	40°
25. Oct. 1938.....	C4	L 4	50	Cloud 10	0·115	3·17	39°
25. Oct. 1938.....	C5	L 3	45	—	0·135	3·45	39°

from the four perpendicular azimuths. But they do not show any evidence of change of average obliquity with depth. In this they agree with the earlier series. As already pointed out (Atkins and Poole, 1940) this approximate constancy of obliquity is probably due to a balance between the opposing effects of absorption and scattering.

Table 5 compares the results of these series with the earlier ones, as arranged in order of increasing values of μ_v. There is evidence for a rise of U/V with increase in μ_v, which of course is what one would expect, since clear water looks much darker than turbid water. U/V is also found to increase in shallow water with a light-coloured bottom. There is, however, no conclusive evidence for a corresponding increase in θ, since the clearest water in C10 showed a high value. Both the 1949 values were rather lower than the earlier ones. Station L3 is off Rame Hd., L5 near the Eddystone, and L4 is intermediate.

At the conclusion of CN22 measurements of the vertical illumination were made with light filters other than green, but no above-water readings of the marine photometer were taken. The mean values of μ_v found are given in Table 6. These may be compared with those for Series C13 and in earlier work.

Table 6

Series CN22, 17. Aug. 1949, 11.50–4.15 GMT. See Table 4

Colour	Ultra violet	Blue	Blue-green	Green	Red
Schott filter.....	UG 1	BG 12	BG12+GG5	VG 9	RG 1
Spectral range (mμ).	320–390	340–480	445–480	480–580	< 600
Depth range (m.)...	1–20	5–40	5–35	5–70	1–20
μ_v	0·227	0·116	0·115	0·101	0·295

We again find a more rapid extinction for blue than for green light. As CLARKE and JAMES (1939) have shown that in pure water green is more rapidly extinguished than blue it is obvious that the difference between pure water and sea water reverses the ratio of the extinctions. An effect due to Rayleigh scattering might greatly increase the extinction in the blue, but filtration through collodion and the study of scattering with a photo-multiplier cell (ATKINS and POOLE, 1952, 1954) suggest that scattering is due chiefly to refraction through transparent mineral particles, large compared with the wave-length of light. It thus appears probable that the reversal and variation in the ratio of the green/blue extinction coefficients is due to absorption by chlorophyll, carotenoids and xanthophylls present in the phytoplankton, aided, perhaps, by some substance in solution in the sea.

Ratio of the Total Illumination to the Vertical Illumination

The rate of photosynthesis in sea water probably depends on the total illumination at the given point, as would be measured by a photometer with a spherical surface. Such an instrument would be inconvenient to handle in rough weather. This total illumination exceeds the vertical illumination by a factor, f, depending on the angular distribution of the light. Thus in air under a uniformly cloudy sky it is easy to see that $f = 2$ plus an allowance for light reflected off the ground or sea. For pure sunlight $f = \text{cosec } \alpha$ where α is the sun's altitude. For midsummer noon at Plymouth with bright sun and clear sky f might be about 1·5, making some allowance for reflected light, while with low sun on 24. January 1934, values as high as 6·0 were obtained with a globe photometer on the laboratory roof (ATKINS and POOLE, 1936). These high values were partly due to light reflected off the sea to the south of the laboratory.

We cannot, of course, calculate f without a knowledge of the angular distribution of the illumination, but the measurements with the cube photometer allow us to make an estimate of its value under water. As the simplifying assumptions that we must make are exceedingly crude it is well to use two different methods.

(1) From the value of H/V we have found θ, the mean angle of obliquity, as given in Tables 3 and 4. If we could replace the existing distribution by a system of rays all of obliquity θ and of any azimuth the total light L would be equal to $V \sec \theta$, so $f = \sec \theta$.

(2) If the illumination were equally distributed over a complete sphere the illumination on one of the plane windows of the cube photometer would be half the total illumination from the hemisphere facing the window, so the sum of the illuminations recorded by the six windows would be 3/2 times the

illumination for the complete sphere. Although the actual angular distribution is very far from uniform it seems reasonable to assume that this is sufficiently represented by the different illuminations recorded for the six windows of the cube, and take $f = 2\,(V + A + B + C + D + U)/3\,V$.

If we apply these approximations to the measurements given at the foot of Tables 3 and 4 we find that for Series CN20 sec $\theta = 1{\cdot}18$, while the second method gives $f = 1{\cdot}21$. For Series CN22 the corresponding figures are 1·23 and 1·29.

It is satisfactory that the two methods give results which only differ by a few per cent. It seems probable that the second method is preferable, as it makes a better allowance for the small amount of light from the lower hemisphere. We may therefore say that the mean value of f for the two series is 1·25. This is appreciably lower than the values 1·35 to 1·65 deduced by Johnson (Jerlov) and Liljequist (1938) from their measurements at Bornö pier in the Gullmar Fjord.

The fact that our measurements do not give any regular variation of the obliquity with depth apparently shows that the decrease with depth of the vertical illumination is a fair measure of the decrease in the total illumination. Moreover, as the average obliquity seems to be only comparatively slightly affected by the daylight conditions above the surface, the value of f under water should only vary over a moderate range, as contrasted with the much larger range occurring above the surface.

Summary

A cubical photometer, used in 1938–1939, was used again in 1946 and 1949. It has six windows, each with a Schott VG 9 (green) colour filter and an opal glass outside. Rectifier photocells occupy the windows, and face upwards, downwards, and in four perpendicular azimuths, respectively. The cells lose sensitivity with time. This necessitates their periodic comparison with a vacuum emission cell, and ultimate replacement. As the loss of sensitivity is more pronounced for strong light, comparison is best carried out in daylight, using colour filters and reducing neutral filters. It may be necessary to correct for the variation of sensitivity with illumination.

As before, the average obliquity of submarine daylight in the waters off Plymouth was found to be between 30° and 40°. This varied little, if at all, with depth below surface, or with surface or daylight conditions, hence the ratio of the total to the vertical illumination in water never differed very much from 1·25. In air it is unlikely to be less than 1·5, and may run up to 5 or 6 with low sun.

Accordingly the ratio (total illumination in water)/(total illumination in air) is equal to the corresponding ratio for the vertical illuminations multiplied by a factor which may vary from about 1·25/1·5 for high sunlight to about 1·25/6 for low sunlight, approximately a fourfold variation.

The upward light, in the rather clear water of these tests, was about 2% of the downward. This agrees well with the earlier results, the percentage rising to 3·5 for more turbid water in October 1938.

Some measurements with other colour filters showed, as before, that green light penetrated best; for though in pure water extinction is a minimum for

blue, the effects of scattering and more especially of the absorption of plankton chlorophyll and yellow pigments cut down the transmission relatively heavily, for both scattering and pigment absorption have less effect on green than on blue light.

Acknowledgements

We desire to thank the Captain and crew of the M.F.V. 1564 for much help in the handling of the photometers, often under difficult conditions, also Mr. F. J. Warren of the Department of General Physiology, Marine Biological Laboratory, Plymouth for his skilful aid in assembling the apparatus and testing the cells, which were also calibrated in the laboratory of the Royal Dublin Society.

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Description of an Improved Rotating Counter for Zooplankton

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The zooplankton counting stage described has been developed directly from a model described by Ward (1955), to enable more rapid examination and counts to be made of the larger larval forms. It can be simply adjusted over a range of speeds, is compact, and easy to operate on AC mains or 12 volt battery.

The counting cell is designed specifically to replace the glass stage of a Cooke, Troughton and Simms binocular microscope Type M6100 (Fig. 1), but, by simple modification, the unit can be used equally well on most low power microscopes. Major parts are machined from Perspex for lightness and ease of manufacture.

The driving disk (see Fig. 2) revolves in a bearing on the baseplate, turned by the rotation of a vertical shaft pressing against its rim. Power is supplied by a small 12 volt motor gearbox unit situated beneath the baseplate.

Over a raised central peg on the driving disk is fitted the sample disk, in which is machined a peripheral groove to contain the sample under examination. The sides of this groove are machined at 60° to prevent settlement of the sample other than on the flat, polished bottom of the trough. Transverse dividing marks are engraved in the trough, and the groove is cut slightly smaller than the width of the field, using the appropriate objectives, to eliminate counting errors. A convenient magnification for general work has been found to be $\times 35$; and $\times 10$ objectives and $\times 10$ eyepieces are used when measuring with an eyepiece micrometer.

Final speed of rotation is $\frac{1}{4}$ R.P.M., but this can be raised or lowered simply by replacing the driving disk with one of greater or lesser diameter. The motor platform is pivoted, and sprung to allow adjustment when a disk of different size is fitted. To ensure the smooth running of the unit, it has been found necessary to increase friction by roughening the edges of the driving disks, and fitting a rubber sleeve on the vertical driving shaft from the motor, but care must still be taken to keep out sample fluid from all bearing surfaces, or rotation of the disks becomes erratic.

Figure 1. Photograph of rotating counter for use with a circular microscope.

Illumination, from beneath the stage, is by a Beck substage illuminator Type 2094, fitted with a rheostat for adjustment of light intensity. For field use, both motor and substage light can be operated satisfactorily from a 12 volt battery.

The motor is started and stopped by a switch, operated by hand or foot, whichever is convenient, and neither action disturbs the position of organisms in the trough. While the speed is usually slow enough to preclude passing part of the sample, it might become necessary to reverse the direction of rotation for recounting, or comparison between organisms in different parts of the trough. In the present model it has been found adequate to move the sample disk

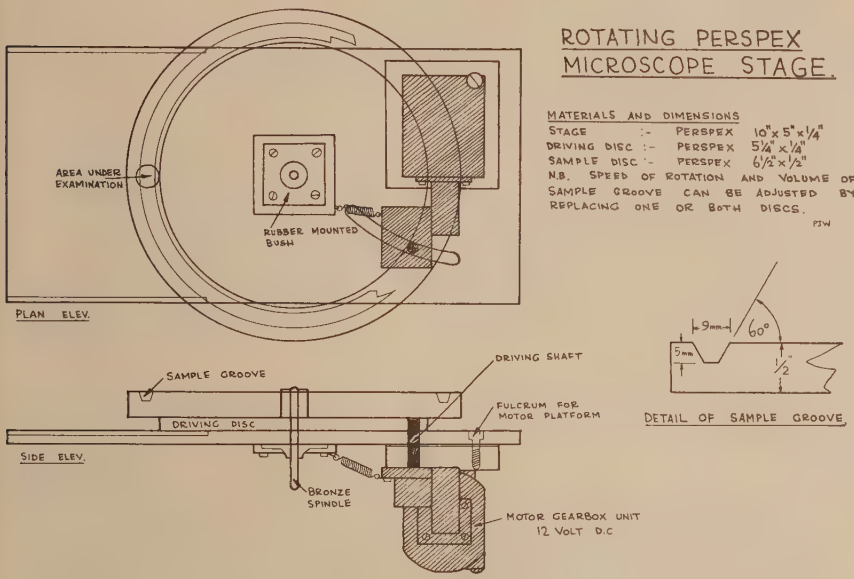

Figure 2. Details of construction of the rotating counter.

backward by hand, and this can also be done without disturbing the sample, but, if necessary, a small gearbox incorporating a reverse gear, or a free pulley positioned between the vertical driving shaft and the rim of the driving disk can be used to do this mechanically.

This unit has proved satisfactory for counting and measuring lamellibranch and *Polydora* larval stages, and counts are straightforward with larvae of similar size in concentrations up to 1,000 per trough of sample holding 20 ml., but it has been found easier to sub-sample more dense samples, using a Stempel pipette, or COLE's automatic pipette and flask.

I am grateful to my colleagues for suggested improvements, and a model having a smaller trough, rotated more slowly, for use with smaller planktonic organisms is now being constructed.

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A Survey of the Larger Zooplankton of Singapore Straits

By

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Introduction

The purpose of the survey was to make acquaintance with the plankton of the region, and to make a basis for a more comprehensive survey, both qualitative and quantitative. Of the different nets used when investigating their suitabilities for the area concerned, only the standard 18 in. coarse tow-net, with 25 meshes to the inch, as supplied by the Plymouth Laboratory, was used regularly, and it is on the catches of this net that the present work is based. Approximately two hauls a week were made, a total of 96 hauls being made during one year.

Regular sampling of tropical plankton for a period of a year from the same area of water has been very limited. The Great Barrier Reef Expedition provided an opportunity for such work, the findings being dealt with by RUSSELL and COLMAN in various reports. Apart from this, the only other series of collections which are comparable appear to be those of THAM (1953). His work was also done in the Straits of Singapore, but his aims, scope, apparatus, and techniques were very different from the present author's, as was the frequency of sampling.

Choice of Station

The station chosen was at the Outer Shoal Light Buoy in Singapore Straits, the position being approximately 1°15′ N., 103°52′ E. It is quite well exposed to such movements of water as occur through the straits, and since the bottom contours, coupled with the swiftness of the tidal flow, ensure mixing of the water, the plankton can be fairly sampled at a single level.

Collection and Analysis

Total hauling time was twenty-one minutes. This consisted of three shorter hauls, each of seven minutes. Tidal flow at the station, sometimes very strong, is usually about 2 to 3 knots, and to ensure reasonable uniformity of sampling, one seven-minute haul was taken against the current, one with it, and one

Table 1

The 14-day periods with the equivalent calendar dates

1	=	1. Jan.	to	14. Jan.	1955	14	=	2. July	to	15. July	1954
2	=	15. Jan.	to	28. Jan.	1954	15	=	16. July	to	29. July	1954
3	=	29. Jan.	to	11. Feb.	1954	16	=	30. July	to	12. Aug.	1954
4	=	12. Feb.	to	25. Feb.	1954	17	=	13. Aug.	to	26. Aug.	1954
5	=	26. Feb.	to	11. Mar.	1954	18	=	27. Aug.	to	9. Sept.	1954
6	=	12. Mar.	to	25. Mar.	1954	19	=	10. Sept.	to	23. Sept.	1954
7	=	26. Mar.	to	8. Apr.	1954	20	=	24. Sept.	to	7. Oct.	1954
8	=	9. Apr.	to	22. Apr.	1954	21	=	8. Oct.	to	21. Oct.	1954
9	=	23. Apr.	to	6. May	1954	22	=	22. Oct.	to	4. Nov.	1954
10	=	7. May	to	20. May	1954	23	=	5. Nov.	to	18. Nov.	1954
11	=	21. May	to	3. June	1954	24	=	19. Nov.	to	2. Dec.	1954
12	=	4. June	to	17. June	1954	25	=	3. Dec.	to	16. Dec.	1954
13	=	18. June	to	1. July	1954	26	=	17. Dec.	to	31. Dec.	1954

across it. The three separate hauls also helped to obviate errors of sampling caused by clogging of the net by the suspended detritus, a constant feature of the water here.

The engine speed was kept constant for every haul so that, irrespective of the speed of the boat over the ground, water passed through the net at about 3·5 knots. This rate of flow, according to the author's experiments at Plymouth, is about the optimum for the grade and size of net used. The timing was taken from the moment the warp became taut until the mouth of the net cleared the water. The catch was immediately preserved in 5% formalin.

The method of analysis was basically that of Russell and Colman (1931, pp. 23–25), i. e., a 1/10 sample was taken from the total catch and completely counted, with a Bogorov counting tray of black glass (Bogorov, 1927). Settled volumes were noted, but due to the generally small size of the plankton, the quantity of suspended matter, and the numerous Siphonophora and Thaliacea often present, they were found to be an uninformative basis for comparisons.

Since the purpose of this paper is to give a general picture of zooplankton fluctuations, the histograms of only the more commonly occurring organisms are shown for twenty-six 14-day periods. The dates of these periods are shown in Table 1. It may be noted that Period 26 contains 15 days, and Period 1 refers to the year 1955; i. e., the samples taken in Period 1 are in fact *subsequent* to those for Periods 2 to 26.

Climatic Aspects

There are no well defined seasons in Singapore. Meteorologically the year is divided into two periods, one in which the North-East Monsoon predominates, and another in which the South-West Monsoon predominates. Tables 2 and 3 show some details of wind and rain during the period under discussion, but it must be remembered that wind and rain can be very local in this area.

Table 2 may suggest that the waters around Singapore are reasonably calm. Usually this is true. However, mainly during the North-East Monsoon, it is possible to have a steady 20–25 knot wind blowing for long periods, and, mainly during the South-West Monsoon, it is not uncommon to have a glass-calm sea succeeded in a few minutes by a "Sumatra" with winds of 40, and sometimes 50 knots.

Table 2

Vector mean surface wind for Singapore

Month	Year	Direction	Speed, m. per sec.
January	1954	360°	1·0
February	1954	20°	1·5
March	1954	40°	0·7
April	1954	300°	0·2
May	1954	230°	0·3
June	1954	200°	1·3
July	1954	190°	0·8
August	1954	190°	1·2
September	1954	200°	1·1
October	1954	250°	0·6
November	1954	320°	1·1
December	1954	10°	1·5
January	1955	40°	2·7

Direction of wind is measured in a clockwise direction from the north.

Table 3

Rainfall (inches) for 7-day periods, Singapore (2. Jan. 1954 to 31. Jan. 1955 inclusive)

Month	Year	1st	2nd	3rd	4th	5th
January	1954	0·83	2·63	0·73	2·16	0·77
February	1954	2·96	2·52	0·06	2·93	–
March	1954	0·46	0·49	0·47	2·09	–
April	1954	0·25	2·04	4·05	2·42	–
May	1954	0·22	0·75	0·95	0·70	0·49
June	1954	4·59	1·74	6·23	2·35	–
July	1954	–	0·66	0·90	0·48	0·85
August	1954	0·93	2·52	5·99	3·83	–
September	1954	0·99	2·91	0·25	0·37	–
October	1954	2·10	2·72	2·00	5·53	4·19
November	1954	1·72	0·37	3·17	4·81	–
December	1954	0·80	15·37	8·91	0·55	–
January	1955	1·96	0·72	1·05	13·05	4·04

The heavy rainfall affects the local waters mainly by varying the turbidity and, over a longer period, by dilution. With the local topography and conditions there is, inevitably, a great deal of suspended matter in the water, the quantity being very variable.

Secchi disk readings were taken with each sample, a 20 cm. disk being used. These readings should be treated with caution owing to the many factors which may affect them; e. g., two readings taken at approximately the same time within fifty yards of each other may show a 50% variation. Figure 1A shows the readings as they were taken and also running averages of five.

Temperatures and Salinities

It was, for many reasons, impossible to take accurate temperature readings in association with salinity measurements at the time of taking the plankton

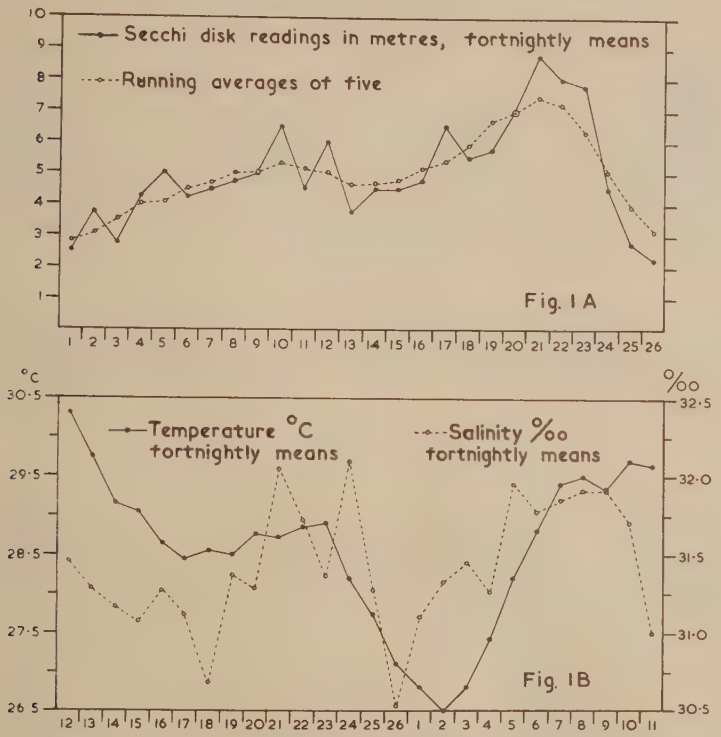

Figure 1. Secchi disk, temperature and salinity readings throughout the observation periods.

samples. Figure 1B has been prepared from data collected between June 1955 and June 1956, during the later survey, and these data have been adjusted to correspond with the 14-day periods to which the plankton histograms relate. The figures used in Figure 1B are the readings taken at 27 m. (the depth of bottom being about 80 m.). This gives a truer picture than surface readings, where both temperature and salinity vary according to daily conditions. A standard Nansen reversing bottle, fitted with two thermometers, was used, and salinities determined using KNUDSEN's method and apparatus.

Comparison of Figure 1B with THAM's figures (1953, pp. 9 and 12) and with readings taken by Dr. F. D. OMMANNEY (unpublished) will show very similar curves, although, with regard to the salinity readings, the range shown here is rather less than that shown by THAM, due no doubt to the fact that his were surface samples.

With four years of readings, taken within a span of eight years, showing such a marked similarity, it is not unreasonable to assume that the basic pattern of salinity and temperature variations during the period to which the plankton samples discussed in this paper refer was the same, or very similar to that shown in Figure 1B.

The Zooplankton

PROTOZOA

Foraminifera

Some of the *Polystomella* type were present at times, no doubt disturbed from the bottom and held in suspension by the water flow.

Cystoflagellata

Noctiluca was not caught in great numbers with the 18 in. tow-net, but maximum numbers occur at Periods 5 and 21.

Tintinnidae

Very rarely found in the net used.

COELENTERATA

(Figure 2A shows total Medusae)

Hydrozoa

Hydroidea. Anthomedusae and Leptomedusae were both present in small, variable numbers. At times numbers of individuals of the Aequoreidae were not uncommon. Actinula larvae were occasionally found.

Trachylina. Variable numbers. Trachymedusan genus *Liriope* Lesson and narcomedusan genus *Solmundella* Haeckel were common at times.

Siphonophora (Fig. 2B). Figure 2B does not represent numbers of individuals, since counts of individuals, nectophores, eudoxids, bracts, etc. were grouped together to give the totals shown. This follows the practice of RUSSELL and COLMAN (1935, p. 256). This group, excepting when Thaliacea were present, formed the bulk of the volume of plankton. As judged from plankton hauls and observations from the boat, only members of the sub-order Calycophora were present. The commonest species seen was, probably, *Diphyes chamissonis* Huxley, common as both individuals and eudoxids.

Scyphozoa

Cubomedusae. Not uncommon at times.

Semaeostomeae. One *Ephyra* larva was found in Period 9.

Ctenophora (Figs. 2C and 2D)

The graph of individual catches (Fig. 2D) shows a fairly regular double maximum throughout the year, with a marked falling off after September. The time intervals between each double maximum are fairly regular, as are the time intervals between each pair of maxima. This can possibly be related to some breeding cycle. There does not appear to be any connexion with moon phases throughout the year. Nearly every individual caught was of the Pleurobrachiidae, with occasional intact or disintegrated individuals of the genus *Beröe* Browne. At various times large *Beröe* were quite common, and individuals about 3 in. long could be seen from the boat at a density of about one per square yard of surface water.

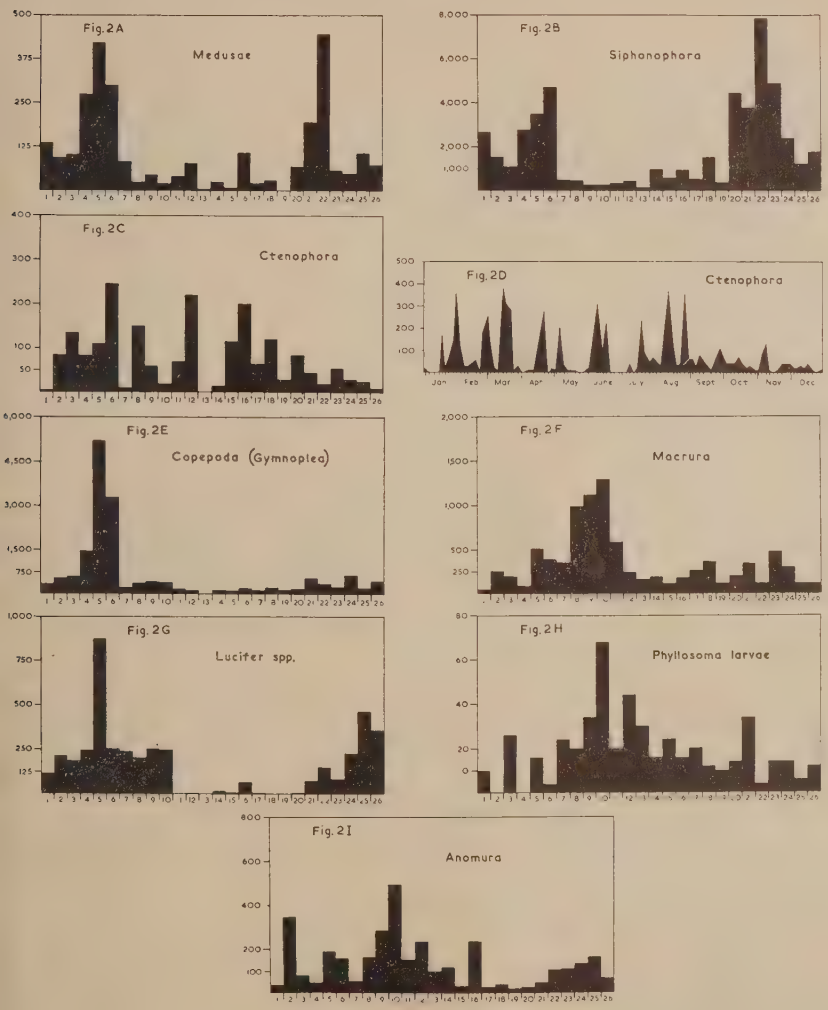

Figure 2. Histograms to show the abundance of zooplankton, expressed as numbers per 21-minute haul, throughout the observation periods.

ANNELIDA

Polychaeta

Tomopteris sp. occurred occasionally, but were never common. Polychaete larvae were present throughout the year, with maxima in Periods 4, 5, and 6. Common among the larvae was a tubiculous form, a terebellid, which had every appearance of being of the genus *Lanice* Malmgren. Hetero-forms were present at times.

ARTHROPODA

Crustacea

Cladocera. Surprisingly rare, only a single species being found in these samples, and that uncommon. For the identification of this species, *Penilia avirostris* Dana, I am indebted to Dr. D. S. JOHNSON of the University of Malaya.

Ostracoda. Not common in these samples, but a maximum period of abundance occurred in late February and early March.

Copepoda (Fig. 2E). It must be pointed out here that while Figure 2E shows, according to the samples, the fluctuations of the gymnoplean copepods throughout one year, the average copepod of these waters is small and would not normally be caught in a 25 mesh per inch net. To illustrate this point, the greatest number caught with the 25 mesh per inch net was about 8,500 individuals; with an N70, 74 mesh per inch net for the same period, with rough corrections to allow for the ratio of aperture to filtering area differences, 150,000 to 200,000 individuals would not be exceptional. Thus, although Figure 2E might well show the fluctuations of copepods in general, in particular it shows the fluctuations of the larger gymnoplean copepods.

Copepoda: Gymnoplea (Fig. 2E). A species of *Eucalanus*, probably *E. subcrassus* Giesbrecht was the most common. It was found throughout the year almost always in juvenile form. During the second quarter of the year *Undinula vulgaris* (Dana) and *Centropages furcatus* (Dana) were common. Various other species occurred throughout the year, the more important being *Euchaeta concinna* Dana and *Labidocera* spp.

Copepoda: Podoplea. Usually too small to be caught with the 18 in. tow-net. However, it was seen, and later verified with finer nets, that the genus *Corycaeus* Dana was the most commonly occurring of the group. Other genera present included *Oncaea* Philippi, *Oithona* Baird, *Sapphirina* J. V. Thompson, and *Copilia* Dana. The two genera *Sapphirina* and *Copilia* were absent most of the year, but were both present in reasonable numbers in October.

Copepoda: Harpacticoida. The genera *Clytemnestra* Dana, *Euterpina* Norman, and *Ectinosoma* Boeck were present; also the spp. *Microsetella rosea* (Dana) and *Macrosetella gracilis* (Dana).

Copepoda: Monstrilloida. Rarely found.

Cirripedia. Nauplii never present in significant numbers in these samples.

Mysidacea. Rare in these samples, but several species, at all stages of development, can be common in bottom plankton hauls at 80 m. particularly at night.

Cumacea. Not commonly found.

Isopoda. Only occasionally present.

Amphipoda. Not common in these samples, but did occur in some abundance in the first half of March. Both gammarid and hyperiid amphipods were found, the latter bing the more common. Oxycephalids were common; caprellids were sometimes found.

Euphausiacea. *Calyptopis* larvae were only occasionally found in this series of samples. However, in the deeper water, all life-history stages are present in bottom plankton. There is probably only a single species concerned; *Pseudoeuphausia latifrons* (G. O. Sars).

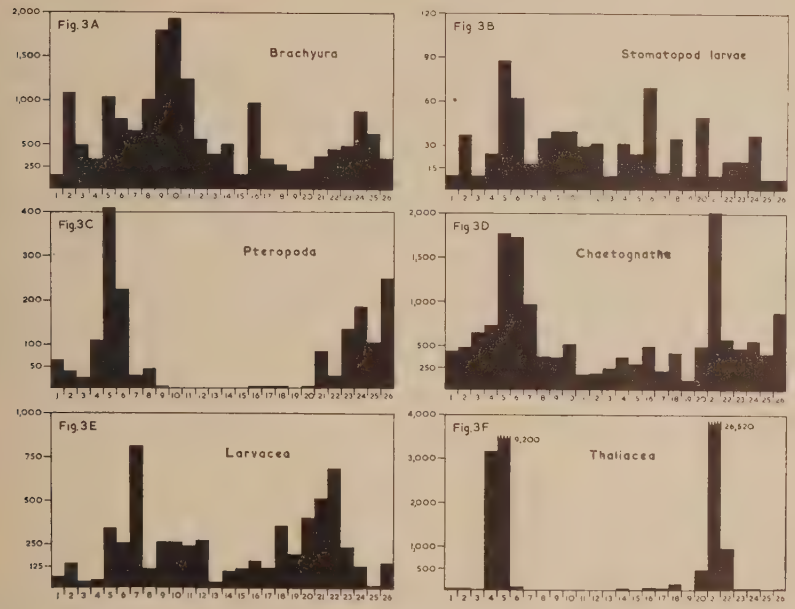

Figure 3. Histograms to show the abundance of zooplankton, expressed as numbers per 21-minute haul, throughout the observation periods.

Decapoda. Macrura. Figure 2F shows numbers of macruran larvae other than *Phyllosoma* larvae. In Singapore waters, the Penaeidea are the dominant form of Macrura, but (*Acetes* H. Milne-Edwards excepted) their larvae are uncommon. Most stages of *Acetes* have been found to be not uncommon, with stenopodid and thalassinid larvae occasionally present, but the caridean larvae formed the greater proportion of the macruran larvae in these hauls. Figure 2G, *Lucifer* spp., shows a marked absence of individuals between Periods 10 and 21. *Phyllosoma* larvae (Fig. 2H) were present throughout the year.

Anomura (Fig. 2I). Although such pagurid and galatheid larvae which did occur are included, Figure 2I is in fact a measure of the abundance of porcellanid larvae, since these were the most common of the anomuran larvae.

Brachyura (Fig. 3A). The larvae of the Brachyrhyncha and Oxyrhyncha were the dominant forms.

Stomatopoda (Fig. 3B). Various types of larvae were found, including *Erichthoidina*, *Erichthus*, and *Alima*.

Arachnida

Pycnogonida. Of the few which were found, some were free, and others were clinging to odd pieces of *Sargassum* weed.

MOLLUSCA

Gastropoda

Heteropoda. Members of the Atlantidae were not uncommon. Only three other heteropods were seen, all probably of the genus *Pterotrachea* Forskal. They occurred in Periods 4 and 5.

Pteropoda (Fig. 3C). There might well be here the possibility of an "Indicator Species", which will show when the water travelling before the North-East Monsoon starts displacing the water around Singapore which arrived with the South-West Monsoon. Figure 3C shows the fluctuations of pteropods as a group, but one species regularly formed the main bulk of the population; Figure 3C therefore shows, in general, the fluctuations of this species also, and hence the term "Indicator Species" can be correctly used here. The predominant species is of the genus *Creseis* Rang, probably *Creseis acicula* Rang. Other types present were *Cavolinia* spp. and *Euclio* sp(p). Of the remaining gastropods found, most were probably small and recently metamorphosed prosobranch larvae. Some veligers were found.

PHORONIDA

Two larvae were found, both on 22. October.

BRACHIOPODA

The larvae are normally too small to be secured with a 25 mesh per inch net. The few which were caught were of *Lingula unguis* (Linné) and what has every appearance of *Pelagodiscus atlanticus* (King).

CHAETOGNATHA (Fig. 3D)

At the beginning of March the dominant species would appear to be *Sagitta enflata* Grassi; of these, a large proportion was mature. At the latter part of the month, the proportion of *S. enflata* to other species had dropped considerably, and there was a larger percentage of immature individuals. During the October period, *S. enflata* was again the dominant species, of which a high percentage was mature.

ECHINODERMATA

The larvae were relatively more abundant in March and October, but in view of the large and varied echinoderm fauna around Singapore, the numbers were surprisingly small. The time of the largest catch, viz., mid-December, corresponds with the period of greatest abundance of Echinoderm larvae found by RUSSELL and COLMAN on the Great Barrier Reef (1934, p. 169). Ophiuroid larvae were the most common.

CHORDATA

Hemichordata

The rarity of *Tornaria* larvae in these samples is surprising in view of the community of adult *Balanoglossus* sp. which lives around Singapore Island.

Urochordata

Larvacea (Fig. 3E). The dominant group was of the genus *Oikopleura* Mertens, but individuals of the genus *Fritillaria* Fol were common at times.

Thaliacea (Fig. 3F). *Salpa democratica* Forskal, which formed the greatest bulk of this group in the samples, has the ability to swarm in enormous numbers with very little prior indication. THAM notes it (1953, p. 28), also SEWELL (1926, p. 120) and RUSSELL and COLMAN (1935, pp. 200–217), who refer to APSTEIN (1894) for other accounts. There does not yet appear to be a completely acceptable explanation for this sudden swarming. Some association with lunar phases has been observed in some cases, but there appears to be no connexion here. The phases of the moon for the period under discussion are:— In 1954, full moon occurred on 19. January, 17. February, 19. March, 18. April, 17. May, 16. June, 16. July, 14. August, 12. September, 12. October, 10. November, and 10. December. In 1955, full moon occurred on 8. January, and a new moon on 24. January.

As additional information, it may be mentioned that in January 1956, the author was on a fishing survey with the research vessel "Manihine", and during the voyage the ship called at Jesselton, British North Borneo. On the night of 14. January the ship was anchored some 150–200 yards off the jetty. To quote from the Log, "About midnight ... a remarkable concentration of salps in the water. Looked at from above there was as much water occupied by salps as not". This extended as far as the eye and a powerful spotlight could reach. By the morning they had, as far as the eye could discern, completely disappeared. There was a new moon on Friday, 13. January.

SEWELL (1926, p. 123) suggests that the primary cause of *Salpa* fluctuations is salinity, the fundamental cause however, being the occurrence of seiches, which govern the salinity variations in the manner he describes. The general structure of the bodies of water with which SEWELL deals is favourable to the formation of seiches. The same cannot be said of the waters in, or adjacent to, the locality in question. In the Singapore Straits, there does not appear to be any obvious relationship between outbursts of salps and salinity or temperature.

The majority of the salps found were aggregate forms, and were parted very easily into individuals. In the actual plankton samples, no two individuals were seen attached, although the chains were clearly visible when swimming in the sea.

Apart from *Salpa democratica*, other species of salps were present in small numbers, as were some species of doliolids.

Cephalochordata

Not found in this series of plankton hauls, but have occurred occasionally in odd hauls. A species of *Amphioxus* not previously described, identified as such by Professor J. E. WEBB of Ibadan University, has been found living in the intertidal zone of eastern Singapore.

VERTEBRATA

Pisces (Figs. 4A, 4B, and 4C)

The relationship between larvae and ova is clearly shown in Figure 4C. This is a line graph obtained by taking averages of five. It is reasonable to

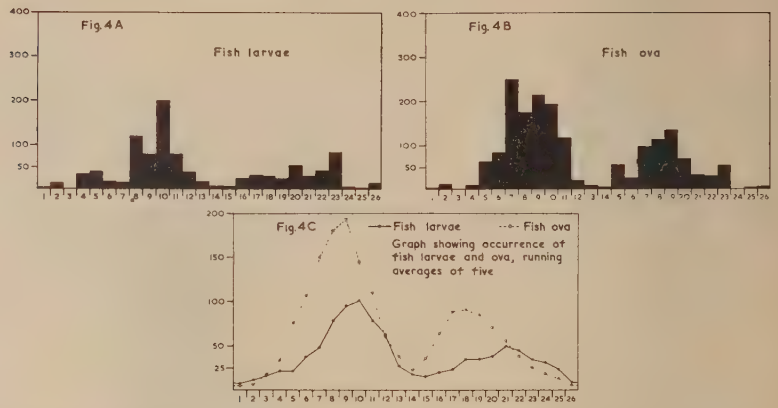

Figure 4. Histograms and graph to show the abundance and relationship between fish eggs and larvae, expressed as numbers per 21-minute haul, throughout the observation periods.

assume that the ova and larvae taken in the samples were different forms of a single component of a plankton community and that the majority of the larvae developed from ova which, earlier, formed part of the same plankton community, there having been no significant addition from external sources, but merely a change in state of a single component. This assumption is supported by the fact that, in general, clupeoid larvae followed clupeoid ova and myctophoidean larvae followed myctophoidean ova. These were the two most common types of ova and larvae. If this assumption is accepted, it can be seen from the graphs that the mortality rate of the fish, passing from ova to larvae of a size which can be caught with a 25 mesh per inch net, is about 50%. Any comparisons with mortality rates of colder water fish must take into account the smaller brood size per given type of fish and the extremely rapid development of ova and larvae to be considered normal for these waters. It is hoped that the later survey will verify this assumption and resolve other points which are suggested by the graphs.

Discussion

In all cases in which sufficient individuals have been collected, with the possible exception of the Ctenophora, there is clearly shown a period of abundance in the first half of the year, followed, in most cases, by a second period of abundance, usually of smaller numbers, occurring towards the end of the year. This, seasonally, approximates to the "spring" and "autumn" growths of plankton in European waters. However, the cause of these periodic fluctuations of the plankton in the Singapore Straits is very different.

When the maximum periods of abundance of the plankton are compared with the maximum readings of temperature and salinity, (Fig. 1B) it would seem that there is a definite relationship, and that temperature and salinity are important causal factors affecting the plankton fluctuations. However,

this relationship can be explained by assuming that the fluctuations of temperature and salinity are not causal but associated factors in respect of plankton fluctuations, these being largely independent of temperature and salinity. This assumes that all are affected by a common factor, which can be seen by referring to Table 2. Here, if change of wind direction is related to plankton fluctuations, the change from the North-East to the South-West Monsoon occurs during the early part of the year, coinciding with the earlier period of plankton abundance. The change from the South-West to the North-East Monsoon occurs during the latter part of the year, coinciding with the second period of plankton abundance.

Detailed discussion of these factors will be held over until the analysis of the larger survey has been completed, but it is suggested that the locality south and south-west of Malaya, including the Straits of Singapore and the Riouw Archipelago, does not have a plankton population dependent upon a continuously changing body of water, but that there are during the course of a year two discrete bodies of water within the limits of the locality given above, each having its own similar but distinct standing plankton population. This can be explained as follows.

At the change-over period from the North-East to the South-West Monsoon, a period several weeks long, the winds are variable, but generally *backing* to south-west. The body of water around the southern tip of the Malay Peninsular and for some distance up the Straits of Malacca is set into circulation with the areas of the South China Sea and Java Sea adjacent to it, and by the time the wind has steadied to south-west, i. e., the South-West Monsoon has set in, this body of water has been replaced by a body of water which has its origin in the Celebes and Banda Sea regions. This water is somewhat diluted during its passage through the Java Sea, but still contains a higher concentration of nutrients, and therefore a larger plankton population, than the body of water which it replaces. This would account for the rise in plankton population during the early part of the year. Due to the steady set of the wind, this body of water, apart from local tidal and other small fluctuations, now remains static, buffered in the north by northern end of the Straits of Malacca and the Indian Ocean. The nutrients are gradually assimilated, with the result that there is a steady decline in the standing plankton population until a state of relative equilibrium is reached (Figs. 5A and 5B). In addition, throughout this period, the heavy precipitation and land drainage gradually dilutes the water and lowers the salinity (Fig. 1B).

It is doubtful whether land drainage enriches the sea to any extent in the region in question. A marked difference of opinion exists between THAM (1953, p. 17) and DELSMAN (1939, p. 149) over this matter. There is not sufficient evidence to decide with regard to local conditions, but in view of the type of ground through which land drainage occurs, it is most unlikely that the quantity of *available* nutrients reaching the sea is able to exert any far-reaching influence on the living population.

Also lasting for several weeks is the change-over period from the South-West to the North-East Monsoon. The winds are variable, but generally *veering* to north-east. This allows the body of water in the region in question to circulate as at the other change-over period until this circulation is stopped by the steadying of the wind to north-east, i. e., the North-East Monsoon has set in. By this time the body of water has been replaced by water coming

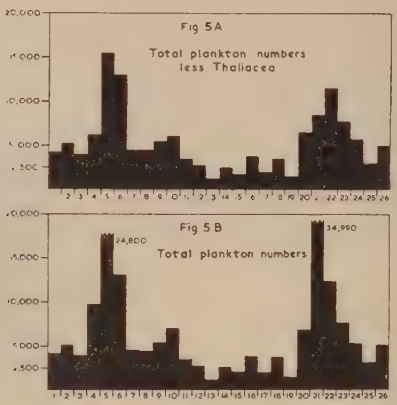

Figure 5. Histograms to show the abundance of the total plankton, expressed as numbers per 21-minute haul, throughout the observation periods.

from the South China Sea, the major part of the displaced water eventually flowing out into the Indian Ocean through the Sunda Straits.

The water entering from the South China Sea is, again, richer in nutrients and more saline than the water which it replaces. Thus, this body of water, with its richer supply of nutrients and the consequently larger plankton population, brings about the second rise in total plankton numbers (Figs. 5A and 5B). As before, this body of water now remains static due to the steady set of the wind and the buffering effect of the northern Malaccan Straits and the Indian Ocean, its nutrient content, standing plankton population, and salinity slowly decreasing until the advent of the change-over period to the South-West commences the cycle once again. This cycle can easily be associated with BERLAGE's suggestion (1927) that "Twice every year the Java Sea is completely swept clean."

In support of the idea outlined above, it is interesting to note that all the animals which form part of the permanent plankton agree very closely in their periods of maximum abundance, which suggests that they all form part of a single entity. (Trachyline medusae form a major part of the Medusae and are to be included in the permanent plankton). The animals, the histograms of which show a departure from the common periods of maximum abundance, particularly the decapod larvae, form the temporary plankton, and as such, can be expected not to conform with the behaviour pattern of the permanent plankton population, but rather to reflect the breeding periods of a fairly fixed community of bottom-dwelling animals.

Acknowledgements

My thanks are due to Professor R. D. PURCHON of the Zoology Department, University of Malaya, for kindly granting facilities to work in his Department; to my colleague, Mr. D. N. F. HALL who did the sampling for me on the occasions when I was not available, and to the Meteorological Department, Singapore, for supplying the meteorological data.

Summary

A description is given of the net and methods of analysis used in sampling the larger zooplankton in Singapore Straits throughout a period of twelve months. A list of the animals which can be expected to be sampled with a 25 mesh per inch net is given, with short notes about each animal or group. Histograms of the more commonly occurring animals show the fluctuations throughout the year, with 14 days as the unit of time. Graphs or tables showing salinities, temperatures, water transparency, rainfall, and wind direction are also given.

It is shown that the fluctuations of the Singapore plankton are similar to the plankton of European waters, and a suggestion is put forward as to the possible causes of the plankton fluctuations in Singapore Straits. The possible water movements south and south-west of the Malay Peninsular are also suggested.

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Plankton in the Western Barents Sea and the Year-Class Strength of the Arcto-Norwegian Cod

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In a recent paper on factors influencing the size of the year-classes in the Arcto-Norwegian stock of cod, WIBORG (1957) considered the numbers and distribution of the eggs and larvae near the spawning areas of the Westfjord and north-western Norwegian coast. He considered that there is no correlation between the abundance of eggs and larvae and the relative strengths of the corresponding year-classes, but he lists as conditions which seem to be important for establishing a rich year-class:— a long spawning period, prolonged hatching or late spawning, an extension or northward displacement of the spawning centre, and a successful transport of the eggs and larvae to the nursery grounds by currents. One factor not included in the list and which is probably important for the survival of larvae is the amount of food available during their pelagic period. This period lasts from hatching in March and April until the "Group 0" cod become demersal about September, and during this time they are dispersed by the currents over a wide area of the Barents Sea, as far north as the north of Spitsbergen and the Great Bank, north-east of Hope Island (CORLETT, 1958a). During this time the food is planktonic and mainly copepods.

During the past nine years that the "Ernest Holt" has been working in the Barents Sea, plankton samples have been taken on most cruises at fixed stations on two lines, west from Bear Island to 13°E. and south from Bear Island to 73°N., and for the last five years more extensive sampling has been carried out over a wider area from 72°30′ N. to 79°30′ N. and from 7° E. to 35° E. Details of the stations near Bear Island and of the other lines of stations and the quantity of zooplankton caught on each cruise for 1949 to 1956, expressed as dry weight, have already been published (CORLETT, 1953, 1958b). For each year a mean value has been calculated to represent the standing stock of zooplankton in the cruises between mid-April and the end of September, that is the months when the cod larvae are pelagic. In Table 1 these means are set out in order of decreasing magnitude and underneath each has been placed

Table 1

Summer plankton stock and cod year-class strength

Plankton dry weight									
(a) Near Bear Island mg./m³.....	54	47	46	34	29	26	24	22	15
(b) North-West Barents Sea g./m².....	–	–	14·5	11·1	9·4	10·4	7·9	–	–
Cod year-class strength.....	very good	good	(good)	–	–	average	(average)	poor	poor
Year.....	1950	1949	1954	1957	1956	1953	1955	1952	1951

N.B. From 1949 to 1952 the plankton samples were usually from 100 metres, and from 1953 to 1957 mostly from the bottom, (average depth 300 metres).
The appreciations in brackets are based on catches of juveniles.

an appreciation of the strength of the corresponding year-class of cod. The year-class appreciation is derived from the Finnmark spring fishery (SÆTERSDAL in WIBORG, 1957), from the "Ernest Holt's" catches in main trawl and cod-end cover (MAFF, 1956, 1957) and from the Russian work in the southern Barents Sea (MASLOV, 1958, USSR, 1957). The year-classes of 1954 and 1955 have not yet entered the fisheries, and the estimates for them are only provisional. The plankton values based on the wider area of the north-western Barents Sea are probably the more reliable indices of the standing stock in the area, but they are available only for the last few years.

It seems from the table that there is a good association between the standing stock of plankton and the strength of the corresponding year-classes. This would suggest that food supply is of some importance in larval survival. It may, of course, be that larval survival and plankton standing stock are influenced independently by some factor such as water temperature or water transport. For instance the two years 1950 and 1954, with high standing stock of zooplankton and good year-classes, were both warm years, hydrographically, in the western Barents Sea (LEE, 1957). HILL and LEE (1958) establish a correlation between the volume transport of the West Spitsbergen Current west of Bear Island and the strength of the southerly wind component during the preceding period: they then show, for the years 1937 to 1941 and 1948 to 1952, an association between the southerly wind component in April and May and the corresponding year-class strength of the Bear Island cod, with the suggestion that when the West Spitsbergen Current is strong the larvae would be expected to reach the nursery grounds quickly. Transport to the nursery grounds must be important, but survival in the pelagic stage during the months of transport depends on planktonic food.

If the association between plankton and year-class strength holds good for a number of years, there is a possibility of predicting the strength of a year-class at a very early stage. This was tentatively suggested two years ago (MAFF, 1956) when it was predicted that the 1954 year-class would be a good one. While it is yet much too early to be sure, there are indications already that this is so. One might further suggest that the year-classes of 1955 and 1956 will be of average strength and that of 1957 above average.

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On Efficiency Tests Made with a Modified Gulf III High-Speed Tow-Net

By

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Introduction

In order to find the most satisfactory net with which to estimate the abundance of post-larval herring, several nets were tested and found to be unsuitable, (Bridger, 1956). All the nets tested were found to catch more young fish by night than by day. With post-larval herring and pilchards this discrepancy increased as the young fish became more developed. It was concluded that from soon after the resorption of the yolk sac they became progressively more efficient in avoiding slowly hauled nets. The remedy seemed to lie in the use of a high-speed tow-net of wide gape, such as the Gulf III tow-net designed by Gehringer (1952). The present paper consists of notes on modifications which have been made to that net, and the results obtained on three cruises to test its efficiency as a sampling device for post-larval herring.

General Description and Modifications

As designed, the net consists of a Monel tube, 5 feet (1·52 m.) in length and 20 inches (50·8 cm.) in diameter, with a conical reducer nosepiece of 16 inches (40·6 cm.) diameter. A tail unit 2 feet (70 cm.) in length and of 16 inches diameter houses the flow-meter and is attached to the body cylinder by means of wing-nuts. Three stabilizing fins are attached to the body casing, which contains a conical Monel "cloth" net. The metal net, on a rigid frame, terminates in a detachable cod-end bucket. Our cylinders were made of 16-gauge iron, which was subsequently galvanized. The flow-meter, which is bolted on to a strut inside the tail unit lies behind the net and so measures the volume of water which actually passes through the net. The original net was of 40-meshes per linear inch, but subsequent nets have been of 60- and 25-mesh. All the catches referred to later in this paper were made with 60-mesh, but filtration tests were made with both 60- and 25-mesh nets.

Three attachments are necessary for the proper functioning of the net: a

depressor to take the net to the required fishing depth; a flow-meter with a capacity of ten times those normally used on vertical nets, and a depth recorder. A footrope "toad" from LARSSON's "Phantom" midwater herring trawl was found to be an excellent depressor. It was attached to a lug on the underside of the towing ring by a 6 foot length of rope. On striking the sea bed the depressor turned sideways, its depressing action ceased and the net tended to rise. By this method, although we occasionally made catches of sand and shingle, we never lost or seriously damaged a net through its striking the bottom.

The flow-meter used was designed and made at Lowestoft, for this and other purposes. Made of brass, it had a capacity of 9,999 units and was similar in size to the Marine Biological Association model, but since it was used horizontally it had no oil-bottle check.

The depth recorder used was an Admiralty pattern of the pressure-operated type. It recorded on a moving roll of waxed paper. The depth recorder was attached by means of a shackle to the towing lug on the net.

Apart from the substitution of galvanized iron for Monel in the casing, two major modifications were made. The first was to attach the tail unit by means of a hinge and hasp instead of by six wing-nuts. This greatly facilitated the removal of the cod-end bucket. The second modification was to reduce the diameter of the nosepiece from 16 to 8 inches; this point will be dealt with in the next section.

Results

I. Sampling technique

(a) Oblique hauls

Two difficulties arose in developing a technique for post-larval surveys. The first was to obtain an oblique haul and the second was to make the net filter efficiently.

The depth of the net in relation to the amount of warp out was obtained with a depth recorder when the net was towed at 5·8 knots. The results are given in Figure 1. The warp used was $2\frac{1}{2}$ inch circumference trawl warp and the net was towed by the R. V. "Platessa" from a boom on the foremast and hauled on the trawl winch. The first attempt to produce an oblique haul was made by shooting the net from the quarter with the ship steaming at 5·8 knots and letting the warp pay out as quickly as possible. As soon as the required amount of warp was veered, it was retrieved very slowly by the winch. This is method A, and Figure 2 shows three typical profiles of hauls made in this way. It will be seen that the net dived steeply and stayed close to the bottom for much of the haul. At the end of the haul it rose to the surface very steeply. As a result, the surface layers were not fished in proportion to those close to the bottom. This could lead to a serious underestimate of abundance if the post-larvae habitually migrated to the surface at some period in the day.

The second method was to reduce the speed of shooting to 180 feet per minute by partially braking the winch drum; the normal hauling speed of the "Platessa's" trawl winch is 180 feet per minute. Thus shooting and hauling speeds were the same and the increased speed of hauling as compared with method A lifted the net clear of the bottom more quickly. By this method, B in Figure 2, hauls were obtained of 4 to 10 minutes duration at most working depths in the southern North Sea, which were to all intents and purposes oblique.

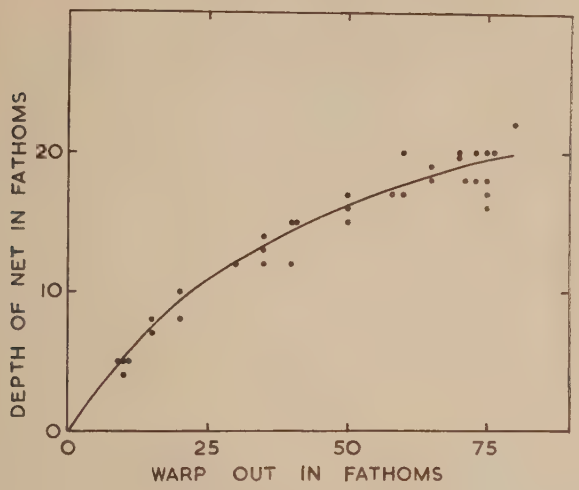

Figure 1. Relationship between warp and depth of the Gulf III high-speed net towed at 5·8 knots.

(b) Efficiency of filtration

Attempts were then made to test the filtration efficiency of the net. To this end a flow-meter was hauled on a Helgoland larva-net frame a number of times from a known depth in calm water. From the mean value of these readings a theoretical value of 4,659 units per nautical mile was calculated. When on the same day, the same flow-meter was put into the empty casing of the net and towed across the tidal stream for 1 nautical mile, measured by the ship's log, the observed reading was 4,608 units. When, however, a 25-mesh net was put into the casing, the flow-meter reading was reduced to 3,544 units per nautical mile. With a 60-mesh net it was reduced still further to 2,028 units. It appeared therefore that the surface area of the net could not efficiently filter the volume of water admitted by the 16 inch nosepiece at 5·8 knots. Since it was impossible to increase the surface area of the net, without building a larger casing in which to house it, a series of smaller nosepieces was made. Hauls were then made over a measured mile across the tidal current in Corton Roads with 8, 11, 13, and 16 inch nosepieces in conjunction with 25- and 60-mesh nets. Hauls

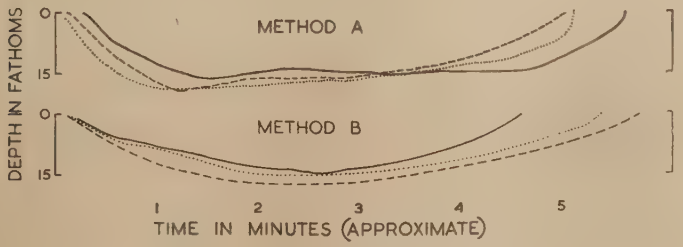

Figure 2. Profiles of hauls made with a Gulf III high-speed net.

Table 1

A comparison of the catches of the modified Gulf III net fitted with 8 and 16 inch nosepieces and a 60-mesh net

Series	Diam. of nose	Flow-meter readings	Fish eggs	Total catch of Post-larval herring III	Post-larval herring IV	*Sagitta* sp.	Ratio of 16″ to 8″ nosepiece Flow-meter readings	Eggs	Post-larval herring III	Post-larval herring IV	*Sagitta* sp.
A	8″	318	294	10	4	40	4·0	3·3	3·1	1·5	1·4
	16″	1265	969	31	6	55					
B	8″	430	302	37	8	54	3·4	4·1	1·4	0·8	0·9
	16″	1480	1232	50	6	49					
C	8″	470	262	13	7	32	2·7	3·2	1·9	1·3	1·2
	16″	1260	839	25	9	38					
D	8″	450	86	16	3	32	3·4	3·2	2·6	4·0	1·5
	16″	1540	278	41	12	49					
						Mean ratios...	3·4	3·4	2·3	1·9	1·2

were also made with no net inside the casing. Figure 3 shows the results of these tests made in very dirty coastal water. A considerable amount of detritus was taken in all the hauls and as later results in offshore water suggest, this materially affected the results, necessitating a smaller nosepiece than would have been necessary in cleaner water. However, it is clear that proper filtration cannot be obtained with a nosepiece of more than 8 inches diameter, where detritus or phytoplankton is abundant.

With a 16 inch nosepiece a considerable wave of water must be built up in the mouth of the net and it was thought that such a "bow wave" might reduce the catching power of the net in one of two ways; it might either wash part of the catch out again, or its presence a short way in front of the net might enable active plankton animals to avoid the net. Accordingly four series of hauls were made between the "Outer Gabbard" Lightvessel and the Brown Ridges on the next cruise to obtain a comparison between the catches of this net fitted with an 8 and a 16 inch nosepiece in conjunction with a 60-mesh net. The catches of these four pairs of hauls are given in Table 1, the young herring being staged as described in an earlier paper (BRIDGER, 1956). Theoretically the 16 inch nosepiece should admit four times the volume of water admitted by the 8 inch. Figure 3, shows that in dirty coastal water, with a 60-mesh net, it filtered only very little more than the 8 inch. In clearer water, the ratio of water filtered per unit fishing time was 3·2 times that of the 8 inch nosepiece. It may be seen from Table 1 that while fish eggs were taken in roughly the same proportion as that of the water filtered, as recorded by the flow-meter, post-larval herring and *Sagitta* sp. were not. This suggested that in spite of its speed some active plankton animals were able to avoid the net fitted with a 16 inch nosepiece. The 8 inch nosepiece appeared to make the net 1·5 and 1·8 times more efficient in the capture of stage III and IV herring, respectively. Whether with an 8 inch nosepiece the net was liable to a further avoidance error could not be determined at that time. Further data on the catches of young herring with a 16 inch nosepiece were, however, available. Thirty-seven hauls had been made, 20 by day and 17 by night, all in the same area on a previous cruise. These hauls yielded 375 stage III and 95 stage IV herring. When an analysis of these hauls was made it was found that at night the mean catches of stage III and IV herring were 1·3 and 1·8 times higher, respectively, than by day. This

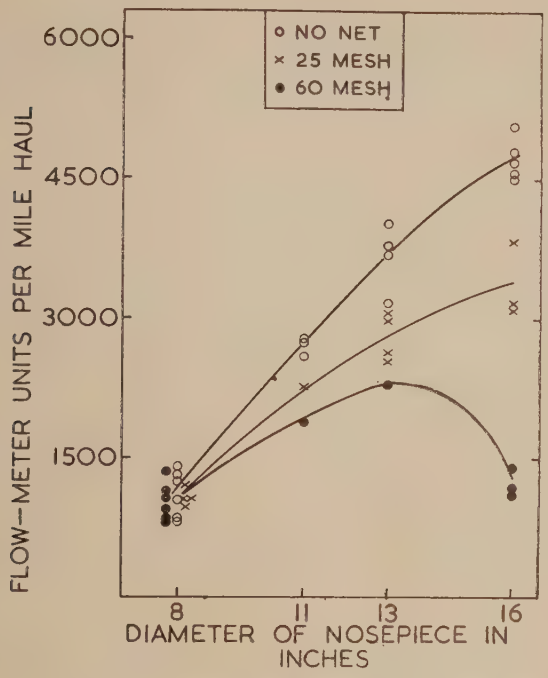

Figure 3. Filtration test on the Gulf III high-speed net.

confirms the view that avoidance of the net with a 16 inch nosepiece did occur and also explained its lower catches when compared with those of the 8 inch nosepiece. Accordingly the smaller nosepiece was invariably used thereafter and an analysis of the catches of the Gulf III net, thus modified, is given in Section IIb below.

This result has a bearing on the only previous report on the catches of this net published in Britain (CUSHING and RICHARDSON, 1956). In that paper the authors reported echo-traces from euphausiids near the surface. From hauls made with a Gulf III net fitted with a 16 inch nosepiece they estimated the concentration of euphausiids responsible for the trace to be as high as 122 per m^3. In arriving at this figure they assumed 100% efficiency, so that their estimate was a minimum. In a later section they compared their catches of euphausiids with those of other authors, assuming 20% efficiency. From our more recent work it seems clear that the filtering efficiency of their gear lay between 30 and 75% and its fishing efficiency for large euphausiids was lower still, dependent on the amount of clogging which occurred. It seems that the authors' estimate of 20% efficiency under such conditions was quite possible, and if that were so then the echo-traces they recorded came from euphausiids in a concentration of up to 600 per m^3. With an 8 inch nosepiece this net may well lead to a new conception of the abundance of the more active planktonic animals.

II. Catches of larval and post-larval herring with an 8 inch nosepiece

Five cruises were made with the "Platessa" during the winters 1954–55 and 1955–56 to test and develop the net. None of the cruises was planned as a survey, but on three of them (I/55, II/56, and IV/56) young herring were caught in fair numbers.

(*a*) *Error occurring in a single observation*

To obtain an estimate of the error liable to occur when only one observation was made, a series of 6 oblique hauls was made at each of 3 stations. The catches, which were of early post-larval herring, were first corrected for the volume of water filtered, as recorded by the flow-meter. These numbers were then transformed by logarithms and the variances computed in the same way as on the catches made with a Helgoland larva net (BRIDGER, 1956). In the first series the variation was 1·52 and 0·67 times the mean catch of 19 post-larvae per haul. This compares very closely with our previous results on the catches of post-larval pilchards made with a Helgoland net, where the variation was 1·57 and 0·63 times the mean of 15 per haul (BRIDGER, 1956). In the two remaining series the mean catches were 9 and 8 post-larvae per haul. The variations in these series were 1·64 and 0·61, and 1·67 and 0·60, respectively. In short, the error on one observation with the Gulf III net is of the same order as the error on one Helgoland haul. The Gulf III net therefore may be accepted as a quantitative plankton net.

(*b*) *Day and night catches*

In all, 96 oblique hauls were made, 47 by night and 49 by day. The catches were preserved separately in 2% formalin in sea water. The young herring were picked out and staged as before (BRIDGER, 1956, Table 1). The total catches of each development stage are given in Table 2, together with the total flow-meter readings. It may be seen that unlike all the nets previously tested the modified Gulf III took as many young herring by day as it did by night. The catches of each development stage taken on each of the three cruises are given in Table 3, together with the flow-meter units and the night/day ratios. These ratios relate the mean catch by night to the mean catch by day. With the exception of the stage V post-larvae on Cruise II/56, on which one was taken by day and none by night, all the ratios fall between 0·37 and 3·63. Their mean value for each development stage and for the collection as a whole is approximately 1. This confirms the supposition that the values of up to 32 in the night/day ratios obtained with slowly hauled nets were due to avoidance of those nets rather than the effect of diurnal migration in taking the young fish out of their range. The Gulf III net was never used, except accidentally, within 4 metres of the sea-bed and so fished precisely the same depth range as the Helgoland larva net, which was found to catch nearly 6 times as many young herring by night as it did by day.

These results also show that the smaller discrepancies observed between night and day catches when the 16 inch nosepiece was used no longer occur. We may conclude that it was imperfect filtration which enabled active animals to avoid the net in its original form. Until it is shown that young herring can avoid a net travelling at 10 feet per second as easily in total darkness as they can by day, the net in its present form may be accepted as truly quantitative.

Table 2

Number of young herring of each development stage taken by day and night

	Development stages						Number of hauls	Flow-meter readings
	I	II	III	IV	V	Total		
Day	6	106	280	133	5	530	49	33,087
Night	5	60	299	116	4	484	47	28,754

Table 3

Range of night/day ratios for each development stage of young herring obtained on three cruises

Actual catch, night	Total flow-meter, night	Actual catch, day	Total flow-meter, day	Catch per 10,000 F.M. units, night	Catch per 10,000 F.M. units, day	Night day ratio	Cruise	Devel. stage
5	6,887	6	11,359	7·26	5·28	1·30	1/55	
–	–	–	–	–	–	–	2/56	I
–	–	–	–	–	–	–	4/56	
60	6,887	106	11,359	87·12	93·32	0·93	1/55	
–	–	–	–	–	–	–	2/56	II
–	–	–	–	–	–	–	4/56	
11	6,887	5	11,359	15·97	4·40	3·63	1/55	
280	14,255	266	13,168	196·42	202·00	0·97	2/56	III
8	7,612	9	8,560	10·51	10·51	1·00	4/56	
1	6,887	2	11,359	1·45	1·76	0·82	1/55	
78	14,255	68	13,168	54·72	51·64	1·06	2/56	IV
37	7,612	63	8,560	59·92	73·60	0·81	4/56	
2	6,887	1	11,359	2·9	0·88	3·30	1/55	
–	14,255	1	13,168	–	0·76	–	2/56	V
2	7,612	3	8,560	1·31	3·50	0·37	4/56	
79	6,887	120	11,359	114·71	105·64	1·09	1/55	
358	14,255	335	13,168	251·14	261·00	0·96	2/56	Total
47	7,612	75	8,560	61·74	87·62	0·70	4/56	catch

III. Vertical distribution of young herring

On Cruises II and IV in 1956, in addition to oblique hauls, surface, midwater, and bottom hauls were made in order to determine whether, at any time of the day the young herring were so restricted to one particular depth that a serious error in estimating their abundance was likely. On these two cruises hauls were made at 4, 10, and 17 fathoms in water ranging in depth from 18 to 22 fathoms. Cruise II occupied 48 hours, the ship being allowed to drift between one series of hauls and the next. Cruise IV occupied 24 hours in the same area three weeks later. All these hauls were made within a radius of 15 miles. Since the net had no closing device each haul was of 5 minutes duration, exclusive of the time taken to shoot and haul. Thus, the surface hauls averaged 6 minutes total fishing time, the midwater hauls 9 minutes, and the bottom hauls 12 minutes. The actual catches of young herring are shown in Figure 4. It should

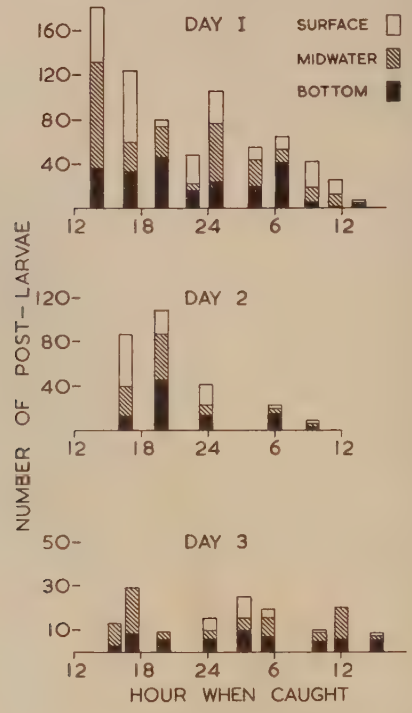

Figure 4. Vertical distribution of post-larval herring.

be noted that no attempt has been made to correct the catches by the flowmeter units recorded, or to calculate what fraction of the midwater and bottom catches were taken on the way down or up. Since each haul is a single observation, and as such liable to considerable error, it seemed pointless to make involved calculations on each one. It must be remembered therefore that the midwater and bottom catches are always an overestimate, especially when the catch at the surface is high. Cruise II was carried out in very dull weather with low cloud and frequent snow squalls. The vertical light intensity on deck measured with an Eel photocell seldom exceeded 10,000 lux and for much of the day lay between 2,000 and 5,000 lux. The catches on these two days are shown under Day 1 and Day 2, in Figure 4. The third day, worked on Cruise IV, was a clear bright day and the light intensity exceeded 10,000 lux from 0900 to 1430 hours GMT; the noon value was 25,000 lux. It may be noticed that whereas on both the grey days a few post-larval herring were taken in the surface hauls throughout the day, under the very much brighter conditions of the third day the surface hauls during daylight hours were virtually blank. The catches consisted of stage III and IV post-larvae and an analysis of the catches of both stages, by depth, was made in order to determine whether their diurnal migration patterns were different. This analysis was complicated by the lack of a suitable closing device for the net. It showed, however, that

in full daylight the bottom hauls yielded a rather higher proportion of stage IV post-larvae than either the surface or the midwater.

This suggests that during daylight hours the older post-larvae were swimming at a greater depth than the younger, but at no time were they so close to the bottom that a serious underestimate would have resulted from making an oblique haul only. This is confirmed by the night/day ratios obtained from the catches in oblique hauls made at the same stations. These ratios, of 0·97 and 1·00 for the stage III post-larvae and 1·06 and 0·81 for the stage IV are given in Table 3. In short, the diurnal migration of young herring up to stage IV (16–25 mm. in length) even on a clear day is unlikely to affect their capture by the modified Gulf III tow-net, provided that an oblique haul is made to within 2 fathoms of the sea-bed.

Summary

1. Experience with a Gulf III all-metal tow-net in the North Sea showed that some modifications were necessary and some difficulties in using the gear had to be overcome before it could be used for larval herring surveys.

2. Tests on the filtration properties of the net showed that its efficiency was increased when the nosepiece was reduced from 16 to 8 inches in diameter.

3. With an 8 inch nosepiece the net was tested and found to catch as many young herring up to 25 mm. in length by day as it did by night. All the nets previously tested, including the Helgoland larva net and the Petersen young-fish trawl failed to do this. For this reason the Modified Gulf III net is the most suitable net yet tested for the estimation of larval and post-larval herring abundance.

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Cod Growth and Temperature

By

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In studying growth phenomena in several species of fish and shellfish, I have found persistent relations between mean temperature conditions and certain growth parameters. These relations for the cod (*Gadus callarias*) seem of possible significance to biologists studying the cod fisheries and are reported here.

Biologists have frequently noted that rapid growth is, in poikilothermic animals at least, generally incompatible with a long life span and, conversely, that large size and a long life span are often associated with the cooler temperatures of high latitudes. Such qualitative conclusions are of limited usefulness, however.

From published age-length data for cod from a number of localities (Table 1), I determined the parameters of the BERTALANFFY (1938) growth equation:

$$L_t = L_\infty (1 - e^{-K(t - t_0)}) \qquad (1)$$

where L_t is the length at time t, L_∞ the maximum attainable size, K a constant related, in its derivation, to catabolism, and t_0 a correction on the time axis.

The parameters L_∞ and K of equation (1) may be estimated by determining the regression of length at time $t + 1$ (L_{t+1}) on length at time t (L_t) (WALFORD, 1946; BEVERTON, 1957):

$$L_{t+1} = mL_t + i \qquad (2)$$

where m is the slope of the regression line and i is the y-intercept:

$$L_\infty = i/(1 - m) \qquad (3)$$

and

$$K = -\log_e m \qquad (4)$$

If one defines life span as the time required to attain some arbitrary fraction, p say, of L_∞, then the life span, A_p, is readily derived from equation (1):

$$A_p = t_0 - \frac{\log_e (1 - p)}{K} \qquad (5)$$

Table 1

Growth parameters for cod from various localities and mean annual surface temperature estimated from World Atlas of Surface Water Temperatures, US Hydrographic Office

Locality	Source of growth data	Mean temp. °C.	Growth parameters K	i	L_∞	$A_{\cdot 95}$
Southern New England..	SCHROEDER, 1930.....	11·5	·281	24·2	98·8	10·7
Nova Scotia	MARTIN, 1953.....	7·5	·118	13·7	123·5	25·4
North Iceland.....	SÆMUNDSSON, 1923	4·6	·064	12·4	200·3	46·9
East Iceland	SÆMUNDSSON, 1923	5·4	·096	13·4	146·6	31·3
South Iceland.....	SÆMUNDSSON, 1923	8·0	·219	21·6	109·6	13·7
South-west Iceland.....	SÆMUNDSSON, 1923	6·7	·147	17·4	127·6	20·4
North-west Iceland	SÆMUNDSSON, 1923	5·6	·080	14·4	188·5	37·7
North Sea	GRAHAM, 1934.....	9·6	·167	22·0	143·5	18·0
Lofoten	ROLLEFSEN, 1934	8·4	·284	23·5	95·9	10·6
North Norway.....	JENSEN and HANSEN, 1931..	6·3	·069	10·2	154·0	43·7
Barents Sea.....	TROUT, 1949.....	5·7	·109	13·8	134·0	27·6

Defining life span as the time required to attain 95% of L_∞ (TAYLOR, in press), equation (5) becomes:

$$A_{\cdot 95} = t_0 + \frac{2{\cdot}996}{K} \qquad (6)$$

Table 1 shows the results of applying equations (1) to (6) to some cod-growth data selected from the literature to cover a wide range of latitudes and temperature conditions. The latter were estimated from information in the World Atlas of Sea Surface Temperatures (Hydrographic Office of the US Navy, 1944).

Annual mean surface temperature is, of course, only a rough indication of the thermal environment of the cod. Furthermore, much excellent growth data for cod exist which have not been used because the monthly temperature information in the World Atlas does not seem sufficiently definitive. This is especially true of areas where sea ice is present during several months of the year (west coast of Greenland), and in areas largely surrounded by land masses or with unusual hydrographic conditions (Skagerak-Kattegat-Baltic Sea areas). It will be noted also that a substantial portion of the data are from the Icelandic area. The hydrographic conditions indicated by surface temperatures around the coast of Iceland appear distinctly different, which makes them as useful for the present analysis as two areas as widely separated, for example, as the southern New England area and the Barents Sea. The differences in growth parameters suggest also, at the time the data were collected at least, a high degree of independence of stocks of cod around Iceland.

On the hypothesis that growth parameters are indices of physiological activity, a linear relation between the logarithm of temperature and the logarithms of the growth parameters K and i might be expected (cf. Q_{10} relations). The expected linearity appeared, (Figures 1 and 2), fitted by the regression equations:

$$\log K = 1{\cdot}6427 \log T - 2{\cdot}2593 \qquad (7)$$

and

$$\log i = 0{\cdot}8573 \log T + 0{\cdot}4973 \qquad (8)$$

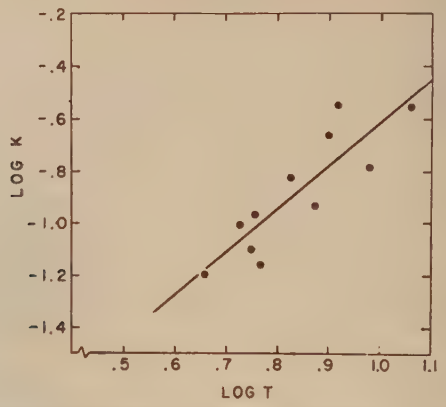

Figure 1. Relation of the growth parameter K (equation 1) to mean annual surface temperature at the localities listed in Table 1.

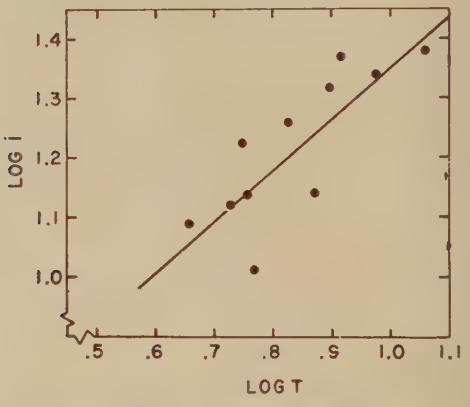

Figure 2. Relation of the growth parameter i (equation 2) to mean annual surface temperature at the localities listed in Table 1.

The correlation coefficient between log T and log K is 0·880; between log T and log i, it is 0·812 (the 1% level of significance, 9 d.f., is 0·735).

Applying equations (7) and (8) to the surface temperature range 4° to 12°C., I have estimated (Table 2) values of i and K and, by means of equations (3), (4), and (6), the corresponding maximum sizes (L_∞) and life spans ($A_{\cdot 95}$). These are shown graphically in Figure 3.

One notes in Table 2 that slight differences in temperature indicate wide differences in expected maximum size and life span. A change in the average annual temperature from 4° to 5°C., for example, produces a decrease in L_∞ of 29 cm. and a decrease in life span of 18 years.

The disappearance of the larger and older fish from an exploited population, and the resulting decrease in the average size of fish caught, is usually attributed

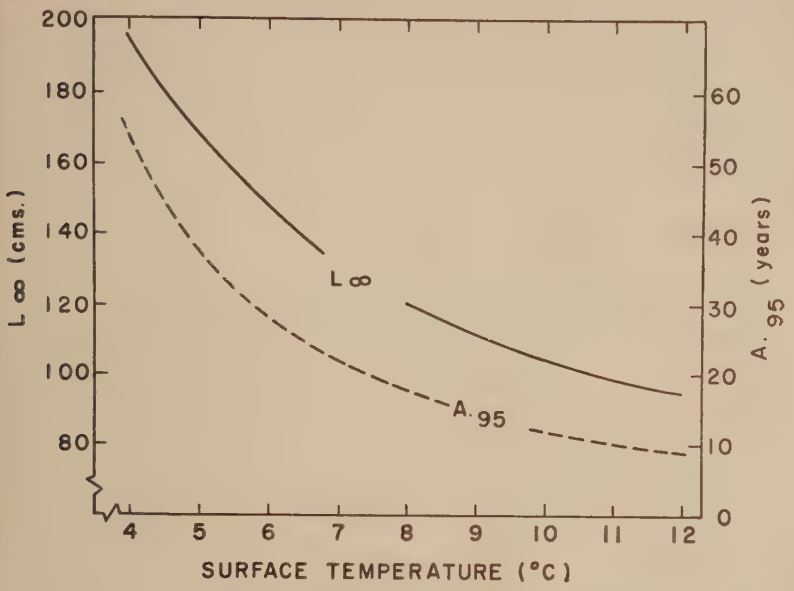

Figure 3. Calculated changes in maximum size (L_∞) and in life span ($A_{.95}$) with surface temperature.

Table 2

Relation of surface temperature on maximum size (L_∞) and life span ($A_{.95}$), as estimated by growth equations (7), (8), and (3), (4), (6)

	Surface temperature, °C.								
	4	5	6	7	8	9	10	11	12
L_∞ (cm.)	196	167	148	132	121	113	105	100	95
$A_{.95}$ (yrs.)	56	38	29	22	18	15	12	11	9

to the effects of fishing. In some instances, at least, equations (7) and (8) suggest we may overestimate the influence of man and underestimate the influence of subtly-expressed but powerful forces at work in nature.

It must be pointed out that major changes in the thermal environment are known to have occurred in northern latitudes in recent times (AHLMANN *et al.*, 1949; TAYLOR, BIGELOW and GRAHAM, 1957). Possibly these changes may have been of sufficient duration and of sufficient magnitude to account for some of the observed changes in the size and age composition of cod populations in certain localities.

Summary

A linear relation between the logarithm of surface temperature and two growth parameters is demonstrated to hold for cod from certain areas ranging from Nantucket Shoals, off the north-east coast of the United States, to Norway and the North Sea. These relations suggest that the parameter K (equation 1)

and i (equation 2) are functions of the environmental temperature of the cod (indicated roughly by the surface temperature). If this is true, it is shown that the maximum size attained (L_∞) and the life span will be considerably affected by slight changes in temperature (Table 2, Figure 3). It is suggested that if such temperature-dependent changes should occur, they might be mistakenly interpreted as effects of fishing.

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Results of English Cod Tagging in the Barents Sea

By

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Introduction

In 1951 and 1952 two tagging experiments were carried out by the "Ernest Holt" on the Spitsbergen Shelf. Their primary aim was to determine the annual movements of the immature cod of the Bear Island shoals, whilst a secondary aim of the earlier experiment was to test two types of tag: the Lea cod tag against the black Petersen opercular button. Numerical data are given and results of the tag comparisons are described in the present paper. Movements of the tagged populations have been described elsewhere and the annual migrations of the immatures derived (TROUT, 1957a).

No tagging was carried out in 1953 but during and after 1954 tagging has been undertaken on most cruises, incidental to the main projects, as part of the Anglo-Norwegian research programme. Some data of the first year's recaptures of the 1954 and 1955 releases are included herein.

The 1951 Experiment

Two main release areas were chosen and fished without encountering commercial fishing. At Hope Island 1995 cod were tagged between 23. and 28. August; 997 with Lea cod tags, attached in front of the first dorsal fin by means of stainless steel, single-ended bridles. The remaining 998 cod were tagged with the black Petersen opercular tag, attached to the left pre-operculum with silver wire in the orthodox manner.

The second release area was at Spitsbergen, on the Hornsund and Sörkapp grounds, from 7. to 12. September. There 658 Lea and 583 Petersen tags were used, bringing the total number of cod released during the cruise to 3,236, i. e., 1655 Lea and 1581 Petersen. (NB. Discrepancies in numbers, e. g., between total numbers released, and length/frequency tables, are due to some lengths of cod not being recorded during the tagging).

Table 1

Total 1951 returns for 6 complete years

Area	Tag	Year of recapture 1	2	3	4	5	6
Hope Island releases	Lea	161	55	26	12	6	3
	Petersen	51	16	4	3	–	–
Spitsbergen releases	Lea	24	22	13	5	5	4
	Petersen	18	4	–	–	–	–

Recaptures made during the six complete years since release are given in Table 1 for each type of tag and for each area. Direct comparisons of these returns cannot, however, be made either between tag types or between areas. Experience at Hope Island showed that the Petersen was too brutal a method to be used for really small cod, whilst the Lea was entirely suitable for cod of 40 cm. and even below. Hence, a certain selection took place during tagging and the tag type was suited to the size of cod. Furthermore, the size composition of the tagged populations in the two areas was markedly different. At Hope Island only few cod of the 40/44 cm. length group were tagged, whereas at Spitsbergen they were the predominant length group on the Hornsund ground. Only Lea tags were used on these small cod.

In order that the data from the two areas may be summed for further analysis they are arranged in 5 cm. length groups. The number of recaptures are shown as percentages of the number released in each 5 cm. length group for first year recaptures only in Table 2 and the summed data for each tag are given in Figure 1.

Table 2

1951 releases and returns per 5 cm. length group (for first year returns only)

Area of release	Tag	5 cm. length groups 25	30	35	40	45	50	55	60	65	70
Hope Island releases	Lea	0	5	47	61	34	35	24	24	57	127
	Petersen	1	1	11	22	23	29	37	39	89	183
Spitsbergen releases	Lea	–	4	81	291	69	23	16	32	45	42
	Petersen	–	–	–	–	–	2	11	46	91	136
Total Lea released		–	9	128	352	103	58	40	56	102	169
% returned		–	–	–	1·7	1·9	5·2	5·0	8·9	11·8	10·0
Total Petersen released		1	1	11	22	23	31	48	85	180	319
% returned		–	–	–	–	–	–	5·0	5·4	4·9	9·5

		75	80	85	90	95	100	105	110	115
Hope Island releases	Lea	195	238	108	34	7	–	–	–	–
	Petersen	253	213	72	18	5	0	0	0	1
Spitsbergen releases	Lea	25	19	7	2	1	0	1	–	–
	Petersen	141	94	49	9	4	–	–	–	–
Total Lea released		220	257	115	36	8	0	1	0	0
% returned		15·9	21·0	33·0	25·0	28·6	–	–	–	–
Total Petersen released		394	307	121	27	9	0	0	0	1
% returned		5·0	9·3	7·0	2·8	–	–	–	–	–

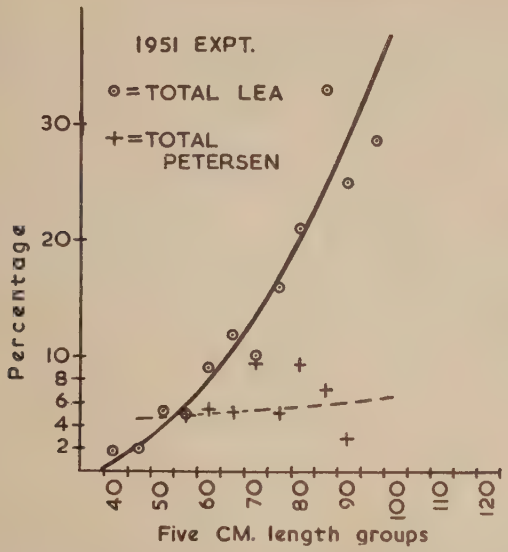

Figure 1. 1951. First year recaptures as percentages of each 5 cm. length group – total numbers of each tag.

A noticeable feature of the first year's returns for 1951 releases was the large number of tags recaptured during the spawning season. Figure 2 shows the recaptures by months, both tags. The remainder of the year brought only a small number each month, hence, the results could be subdivided roughly into two seasons which coincided with two geographical regions: (a) winter and early spring; the spawning season on the Norwegian coast and the approaches thereto, and (b) the summer and autumn on the more distant feeding grounds and the approaches thereto.

Besides the seasonal differences another major difference exists between the areas. The Norwegian coast is the scene of the great traditional "Skrei" fishery, carried out by several different gears. In addition, the outer banks, e. g., Malangensgrund and Andenes, are fished by trawlers of several nations during the spawning migration. The first area is therefore one of mixed gears. The more distant banks of the Barents Sea, including Bear Island, Hope Island, Skolpen Bank, and Goose Bank are almost wholly areas of heavy trawl fisheries.

The data were analysed, therefore, by areas into (i) "Norwegian coast" and (ii) "other banks" (Figure 3), and also by gears, into (i) trawl recaptures and (ii) recaptures by all other gears (Figure 4). These figures are based upon first year returns of the 1951 releases and, in the absence of lengths at recapture, their release lengths, in 5 cm. length groups.

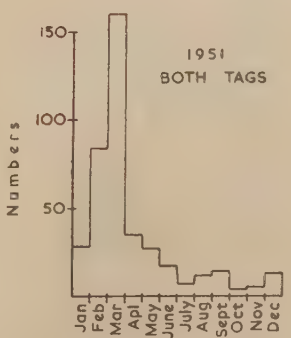

Figure 2. 1951. Total numbers of both tags, by months.

Table 3

1952 releases and returns per 5 cm. length group for first year 1951 returns for comparison of black and yellow Petersen tags

1952 Petersen (yellow)	5 cm. length groups												
	40	45	50	55	60	65	70	75	80	85	90	95	100
Plain button releases	14	469	634	270	157	109	108	104	73	39	6	1	3
Flagged button releases	10	416	639	298	177	99	126	104	77	51	16	6	4
Flagged ..... No.	0	6	24	11	13	7	8	7	12	11	0	1	0
Recaptures ..... %	–	1·4	3·7	3·6	7·3	7·1	6·4	6·8	15·6	21·6	–	16·6	–
Plain ..... No.	0	8	16	10	5	5	5	6	1	3	0	0	0
Recaptures ..... %	–	1·7	2·5	3·7	3·2	4·6	4·6	5·8	1·3	7·7	–	–	–
1951 Petersen (black) .. No.	–	–	–	2	3	5	16	11	24	8	1	–	–
Recaptures ..... %	–	–	–	5·0	5·4	4·9	9·5	5·0	9·3	7·0	2·8	–	–

The 1952 Experiment

The obvious superiority of the Lea tag was shown up in the first year of returns and it was chosen for future tagging programmes. Lea tags, however, could not be obtained in time for the 1952 June cruise, and Petersen tags were substituted, this time in bright yellow "Ivorine". The main aim was again to determine, in more detail, the summer movements of the Bear Island shoals. In addition, secondary aims were (a) to investigate the poor showing of the Petersen tag and (b) to attempt to improve the supply of information accompanying tags by using a more readily seen message than that carried by the Lea. It had been found in 1951 that approximately 65% of all Lea tags were returned unopened — the message therefore unread. Printed paper slips in polythene envelopes 5 cm. × 1 cm. were therefore stuck to the yellow buttons in alternate hundreds. These flags lay along the gill cover when the buttons were attached in the usual manner and did not appear to affect the cod in any way. (The text could be read without removing the tag.) Work-hardening, soft annealed stainless steel wire was used in place of silver wire.

A total of 4,121 cod were released in three areas in June close to Bear Island. Length compositions of plain and flagged populations and their returns are given in Table 3. In the first two areas, the N.W. Gully and S.S.W. of Cape Bull, tagging took place on small fish in exceptionally poor physiological condition. Between 20 and 30 trawlers of several countries were also fishing these grounds. The third area, S.S.E. of Cape Bull, contained no trawlers and was characterized by the presence of larger fish in good condition.

Returns for the five complete years since release are shown in Table 4 for

Table 4

1952 plain/flagged Petersen comparison

(numbers of fish recaptured)

1952	Year of recapture				
	1	2	3	4	5
Plain yellow buttons	60	20	8	5	0
Flagged yellow buttons	103	35	15	6	2
Flagged returns ..... %	63·0	63·6	65·2	–	–

plain and flagged buttons. No direct test was made between black and plain yellow Petersen tags, but data from the two experiments have been arranged in a comparable manner, Table 3, and it is thought that such a comparison is valid.

Comparison of Results from the two Experiments

(i) 1951 Lea/Petersen comparison

Returns for the six years show a gross ratio of 3·5 to 1 in favour of the Lea. From the Hope Island releases, where each tagged population had roughly comparable length compositions, the first year gave 3·16:1, the second year 3·44:1 (Table 1). A rapid increase in effectiveness of the Lea occurred subsequently, whilst no Petersen returns were made for the last two years. In addition to the black Petersen tag proving less effective, presumably due to poor visibility of the black button, there was evidence that they were either shed or, in some cases, overgrown by tissue.

(ii) 1951/1952 Petersen comparison

There is apparently no significant difference in the efficiency of the yellow over the black button — in fact the 1951 results are better than those of 1952. This is thought to be due to the very poor condition of the cod in June, mentioned earlier, when the probably heavy post-tagging mortality could have masked any improvement expected from the higher visibility of the yellow button (Table 3).

(iii) 1952 plain flagged Petersen comparison

Visibility undoubtedly improved with the use of the message flag and gave a remarkably constant difference in percentage return of the two types. This remained for the first three years 63·0%; 63·6% and 65·2% of the yearly total of recaptures (Table 4).

(iv) 1952 flagged Petersen button returns

Individual English ships and skippers were circularized by letter at the beginning of the tagging experiment in 1951 and publicity was continued in 1952. In addition to the usual request for recapture position and date, the flat message flag asked for the fish to be kept—so that growth and age data might be obtained. Table 5 gives the number of instances in which the request was carried out. A comparison can be made with the returns from the plain button tag. It will be seen that, in the first year, there was a significant difference between the number of whole fish returned to the Laboratory with the flagged and the plain button. It was also evident that publicity had had its effect — as shown by the return of fish with plain buttons. In later years the difference between the two types was not so high, probably because the habit of keeping the fish had become more widely established. A further value of this type of flat message lies in the fact that the text can be altered, readily, to meet the specific requirements of a new or modified tagging programme.

Table 5

1952 experiment. Number of yellow Petersen tags accompanied by fish or fish length and otoliths

Year	Plain button		Flagged button	
	With fish or otoliths	Tag only	With fish or otoliths	Tag only
1.....	38	22	77	26
2.....	17	3	29	6
3.....	7	1	13	2
4.....	2	3	5	1
5.....	–	–	1	1

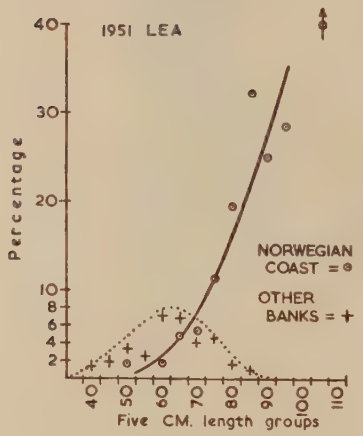

Figure 3.

Figure 3. 1951. By areas. First year recaptures of Lea tags only, as percentages of each 5 cm. length group.

Figure 4. 1951. By gears. First year recaptures of Lea tags only, as percentages of each 5 cm. length group.

Figure 5. 1955. By gears. First year recaptures of Lea tags as percentages of each 5 cm. length group.

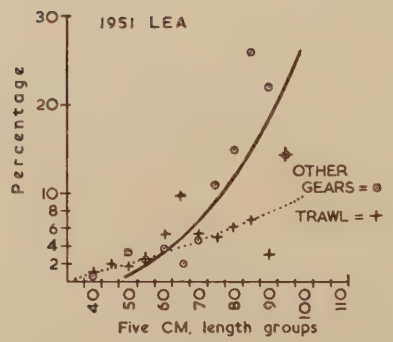

Figure 4.

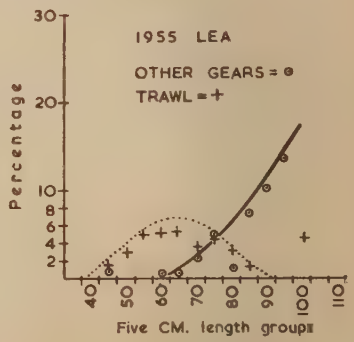

Figure 5.

Table 6

1951 releases. Numbers of fish recaptured, by countries

Country	Year of recapture 1	2	3	4	5	6
Faroes	3	1	1	–	–	–
Germany	23	7	2	1	1	3
Iceland	1	–	–	–	–	–
Norway	162	68	28	15	8	3
United Kingdom	58	13	9	3	2	1
USSR	9	6	3	1	–	-

Table 7

1954 and 1955 releases. Numbers of fish recaptured in first year after release, by countries

Country	1954 releases Trawl	Other gears	Year 1 totals	1955 releases Trawl	Other gears	Year 1 totals
Faroes	1	–	1	6	–	6
France	1	–	1	1	–	1
Germany	9	–	9	20	–	20
Iceland	–	–	–	1	–	1
Norway	15	25	40	29	47	76
Spain	–	–	–	9	–	9
United Kingdom	42	–	42	79	–	79
USSR	7	–	7	8	–	8

Discussion

It appears probable that two main factors are responsible for the "area/gear" differences seen in this analysis — a biological factor and a gear effect.

Area. Norwegian coast returns are seen (Figure 3) to increase markedly with length and indeed it is to be expected that a high proportion of a tagged population containing large numbers of cod over 70 cm. would be caught during the intensive traditional Norwegian "Skrei" fishery. That the length composition itself is important is brought out clearly in Tables 6 and 7" returns by countries" for 1951 and for 1954/1955. There has been, previously, some speculation as to the efficiency of the reporting of tagged fish in some countries. During DANNEVIG's 1947–1953 tagging experiments, where over 4,300 mature cod of 100 cm. or more were released, United Kingdom trawlers returned only 14 of these cod in the seven years. (I wish to acknowledge DANNEVIG's kindness in providing these data at the 1955 Bergen Meeting.) Reference to Table 2 will show that the 1951 tagged population contained some 60% of cod more than 70 cm. in length. In contrast are the returns for the first years of 1954 and 1955, when predominantly small cod were tagged (TROUT, 1957b). Recaptures within the "Skrei" fishery dropped from the 1951 figure of 63% of the total number recaptured in the first year, to 23% in 1955, for gears other than the trawl (see Table 7).

Gears. Separation of both 1951 and 1955 results into recaptures by (a) trawl and (b) other gears, Figures 4 and 5, demonstrates the greater effectiveness

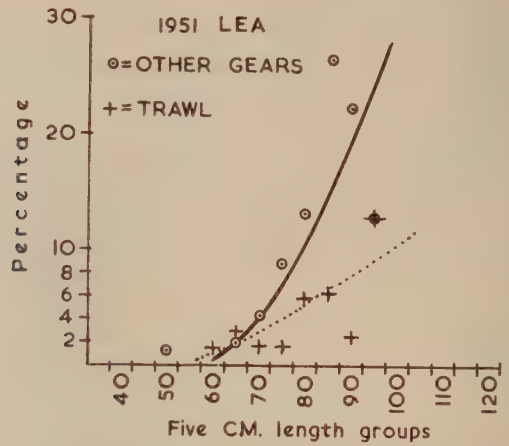

Figure 6. 1951. By gears. Norwegian coast only. First year recaptures of Lea tags as percentages of each 5 cm. length group.

of the latter in catching the larger length groups. The trawl appears to have, in effect, a selective action in point of size, at the upper as well as the lower size ranges of the population. The reason for the similarity between Figure 3 and Figure 5 is that the bulk of the 1955 first year recaptures were made on the feeding grounds. The curve thus tends to be an "area" curve.

There are probably two factors which bring this about. Firstly, a biological one: on the feeding grounds away from the spawning area, the cod, at least on the Spitsbergen Shelf, is diurnally pelagic (TROUT, 1957a). The length of the pelagic period increases progressively with the increase in penetration of daylight in the earlier part of the year, even when the cod are not yet feeding actively upon their largely pelagic, or bathypelagic, food. Thus the cod are less vulnerable to the trawl, since they spend a considerable time above the height at which the headline fishes. This is well known in echo-sounding surveys. Echo surveys have also encountered conditions of high signal count but low catch. When such catches have contained a few large fish it appears possible that more large fish were on the ground but were able to escape the trawl, or were sufficiently far above the bottom to avoid the headline. Mere size, and so possibly speed, could enable them to avoid the net.

Secondly, there may be a physical effect dependent upon filtration of the trawl and therefore upon mesh size. ROLLEFSEN (1953) has shown that in the spawning fishery at Lofoten, cod taken by different gears differ in size — the purse seine takes the largest fish and the longline the smallest. At Greenland, in 1952, the "Ernest Holt's" trawl caught cod of one age-group with a mean length 3 cm. lower than those of the same age-group taken by lines — 67·0 cm. against 70·2 cm. for the 1945 year-class — here again suggesting that the trawl, even with 110 mm. mesh, has a lower size selection.

This difference between the gears persists even on the Norwegian coast (Figure 6) so that it is not due to an area bias. The comparison must not be pressed too far, however, because there are, within the Norwegian coast region, two entirely different fisheries; (a) on the outer banks where the cod are on

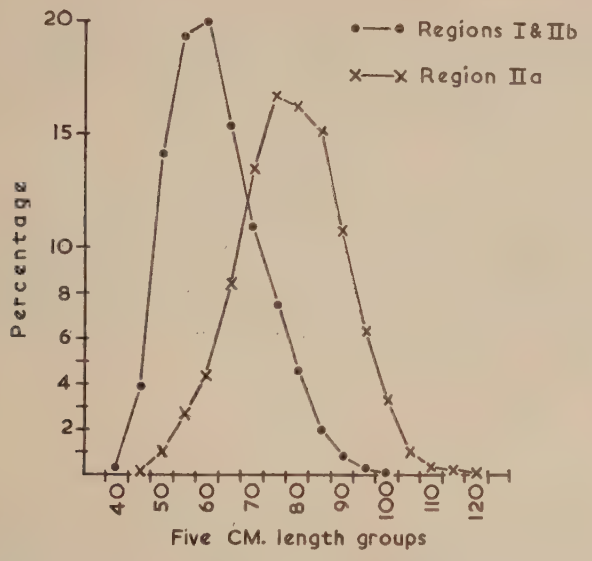

Figure 7. Mean lengths of cod landed from Regions I and IIb and from Region IIa (Norwegian coast), respectively. Hull and Grimsby market measurements 1951–1955 inclusive.

the bottom and (b) in the fjords and sounds where the cod are pelagic during spawning and where they are not, of course, subjected to a trawl fishery.

Figure 7 gives the mean length composition of the English landings at Hull and Grimsby for the two main areas, i. e., the feeding grounds of the Spitsbergen Shelf and South-East Barents Sea and the grounds over which the spawning migration takes place — Regions I and IIb and Region IIa, respectively.

Davis (1934) first showed that by increasing the mesh of a trawl, the catch tended to be greater and also there was a greater number of larger fish in the catch. It would appear possible that a mesh size greater than 110 mm. could reduce the disparity in size of cod caught by the trawl compared with other gears in the areas discussed and also effect a reduction in mortality amongst the lower and less valuable size groups.

Summary

1. The Lea tag is shown to be superior to the Petersen.

2. The rate of return of the Lea tag and therefore of fishing mortality increases with the length of cod.

3. It follows that in treatment of tagging data it is essential that the length composition of the tagged and recaptured populations should be taken into account. An overall percentage of recapture can be misleading and may frequently be of little value.

4. The size difference of cod caught by trawl and by other gears is demonstrated.

5. It follows that method of recapture should also be taken into account when dealing with returns from fisheries carried out by mixed gears.

6. The advantages of a readily seen message flag are demonstrated.

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On the Interpretation of the East Anglian Herring Data 1923—1955

By

W. C. Hodgson

The unprecedented changes which affected the East Anglian herring stock in the years following 1951 are by now well known. I described the events of that period in a series of articles in *World Fishing* in January, February, and March 1956, and I also outlined the problem in *The New Scientist* Vol. 1, No. 2, 1956. Further detailed arguments appeared in "The Herring and its Fishery" (Routledge & Kegan Paul, London, 1957).

Briefly, my interpretation of the data which I had collected between 1923 and 1955 was that from 1951 onwards, recruitment to the shoals was interfered with by the Industrial Fishery for immature herrings on the nursery grounds, and also that the average annual rate of decrease as observed in the older fish, rose after 1951 by about nine or ten per cent. It was shown that the non-appearance of those herrings that matured in their fourth year altered the ratio of the three- to four-year-old fish in the shoals, making the three's more numerous than the four's of the same year-class, and at the same time, the average number of four's in the shoals during the period 1951–55 was very much reduced in comparison with the average for 1946–50. The reduction was in the proportion of 19:12 or 37%, which meant that the "Capital" from which the adult stock was produced was reduced before natural and fishing mortalities took their toll. This reduction, which I attribute to the fishery for immatures, is further aggravated by the apparent rise in the percentage annual rate of decrease of the adult fish with the inevitable result that the "November" fishery at East Anglia which primarily depends on these adult fish, has failed.

Other investigators have different views which point to "Natural Causes" coupled with excessive trawling of the adults rather than the fishery for immatures as being the main reason for the East Anglian decline, and it is my intention to examine critically the reasoning that has led to these findings.

For many years I had calculated the relative strengths of the year-classes for the purpose of forecasting the fishery, and in 1951 the forecast of the four-year-old fish failed for the first time. This group, as it appeared in the fishery, was very much less abundant than it should have been and at the same time these same fish increased in length. In the following years the four's continued

to fail and the increase in their length was maintained, and in 1952, 1953, and 1954 three large year-classes appeared as three-year-olds. That was the sequence of events at the beginning of the change.

The sudden increase in the length of the fish and the reversal of the 3:4 age-group ratios led at once to the alternative theory of advanced maturation, and it was argued that because the fish grew bigger they matured earlier, therefore more came into the spawning shoals as three's and by 1952, when the "change" was complete, there came the large three-year-old group into the shoals followed by others in the next two years. KREFFT, SCHUBERT, and SAHRHAGE referred to this change as "rejuvenation" and the Danish Fisheries Research Institute, in a letter to the Editor of "World Fishing" in 1956, also ascribed the change to advanced maturity, saying that "the increased growth-rate of the herring supports this view." CUSHING and BURD, in their report "On the Herring of the Southern North Sea" (Fish. Invest., Ser. 2, **20** (11)) also came to the conclusion that the advance in maturity was responsible for the change but they no longer consider it merely as a possibility. They treat it as an established fact.

Let us look closely at the data as presented by CUSHING and BURD and follow their reasoning step by step.

1. Environment

They first of all show that the numbers of *Calanus* as estimated on the "Flamborough Line" rose sharply in 1950, and claim that a high number was sustained during subsequent years. This phenomenon they associate with the increase in length of the three's in 1950 — due to better feeding — and of the older fish in the following year, but it is difficult to follow this alleged association from the data. It is true that the East Anglian three's increased in length at the same time as the *Calanus* increased in numbers, but the three's of the next four years were also big although the *Calanus* level was falling rapidly. By 1952 this level was the same as it was in 1948 and 1935 when the length of the three's was quite small. A further discrepancy is that while the three-year-old fish were supposed to have flourished well in 1950, the four-year-olds of that year *were the smallest for many years*. CUSHING and BURD do not explain this, but only make the general statement that the three-year-olds increased in length in 1950 and the older fish did so in 1951.

Looking at their Figure II, 3, especially at the data for Boulogne and Ostend, there is a clear impression that the increase in length of the three's between 1949 and 1950 was followed by an increase in the four's of the following year and of the five's in the year after that. The sixes and sevens do not show this so clearly which, considering the fact that we are dealing with average lengths, is not surprising. Thus it appears that what really happened was that each year-class from that of 1947 onwards increased in length, which would make the supposed association with the numbers of *Calanus* extremely doubtful. In their Table 1, CUSHING and BURD have shown that the greatest length increment between the ages of 3–4, 4–5, and 5–6 in the East Anglian fish occurred in 1951. Now, the considerable increase in the length of the four's of that year could quite easily have affected the average size of the fives and sixes with which they were swimming, and it must not be overlooked that the

data from Boulogne and Ostend (Figure II, 3) do not support the findings of Table 1.

Next, there is the case of the herrings from the northern North Sea as shown by CUSHING and BURD in their Figure II, 4. Here, the length pattern during the years 1951–54 is seen to be quite different from that of the herrings further south, the three-year-olds being abnormally large in one season only — 1952. These fish were apparently unaffected by the great abundance of *Calanus* in 1950 because their mean length was low in that year, and in this connexion it is important to note that *the three-year-old herrings of the Northumberland coast had a length pattern almost identical with the Fladen fish during the years 1949–53.* BURD has described the changing length of the latter herrings in *Annales Biologiques*, Vol. X, 1953, and his Figure 20 shows that, like the Fladen fish, the length in 1950 was small, and was, in 1952 very big. The importance of this evidence, which is not given in CUSHING and BURD's report, lies in the fact that off the Northumberland coast there is the greatest herring feeding ground of the southern North Sea, and certainly the nearest one to the "Flamborough Line" from which the *Calanus* data were obtained. Is it not remarkable, therefore, that the superabundance of *Calanus* in 1950, which was supposed to have affected the East Anglian three's of that year, should have had no effect whatever on the herrings of the same age that were actually on the feeding ground? From the foregoing, it is reasonable to conclude that the increase in size of the herrings is unconnected with the rise in numbers of *Calanus* on the Flamborough Line in 1950.

2. Advanced Maturity

CUSHING and BURD have attempted to show, in two ways, that an advance in maturation actually did take place: (1) by comparing the l_1 distributions of the three- and four-year-olds before and after 1950–51, and (2) by calculating the total number of recruits at each age over a long period of years and estimating the percentage of three-year-olds in this number for each year.

It is a well-known phenomenon that the mean length l_1 of our four-year-old herrings is less than the mean length l_1 as calculated from the three's, and there is no need to enlarge on this fact here. When I first noticed the lack of four-year-old fish in 1951, I applied what might be called the "l_1 test" to my material and found that the difference between the mean l_1 of the four's of 1951 and the mean l_1 of the three's of 1950 was smaller than in the other previous year-classes, which suggested that something abnormal was taking place. CUSHING and BURD have used this same phenomenon to show that the fish matured earlier, but their reasoning is open to criticism. In their Figure II, 5 they show that between 1948 and 1949 and between 1949 and 1950 the l_1's of the three's and four's were different but after 1952 the distributions were very similar.

If, they say, the advance in maturity was completed in 1952, one might expect that, as the smaller fish with small l_1's would come in then as three-year-olds then there would be no difference between the l_1 distributions of the three-year-olds and four-year-olds of the same year-class. But, as they have said in *Nature*, Vol. 178, July 1956, and also in their present report, 1952 was the first year when the three-year-old herrings have had better feeding conditions *throughout the whole of their life* (accompanied, they claim, by better growth),

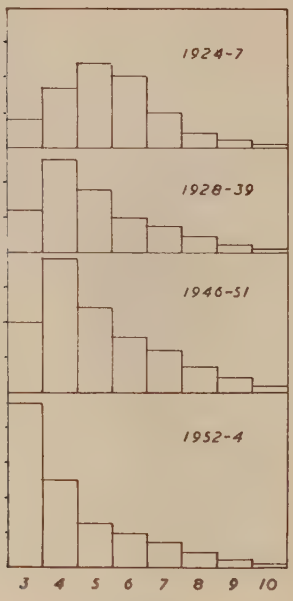

Figure 1.

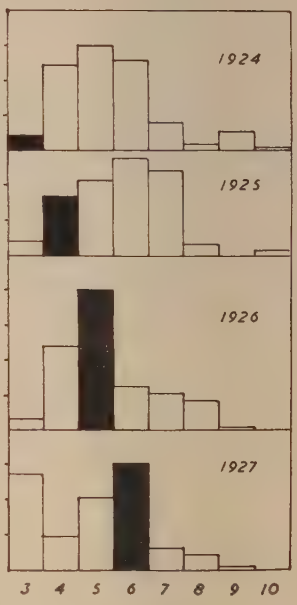

Figure 2.

so how can this statement be reconciled with the fact that there were more small l_1's in the three-year-olds than before. A further point is made from their Figure II, 5. They claim that because the l_1 peak in the three's in 1953 (1950 year-class) was at 10–11 cm. and in 1952 it was at 9 cm. and that this increase has since been sustained, it is evidence that the fish in their first year increased in length at the same time as the older fish, i. e., in 1950. If this is true, we must ask why the l_1 of the three's in 1948 and 1949 (their Figure II, 5) were also big before there was any question of either good feeding or early maturity.

What CUSHING and BURD have ommitted to point out is that the phenomenon they describe could equally well have been produced by interference with the four-year-old recruits to East Anglia which is the reason I give for the changes. This, however, is not the only confusion over the length l_1 and the central zone of the herring scale, for in "Sea Fisheries Research Notes, 1956" (Min. Agric. Fish. and Food) it is stated that a high proportion of herrings with scales of the East Anglian type — *small* centres — on the Bløden Ground, was taken as a good sign for the October East Anglian fishery, but in the next paragraph we read that the scale type of the East Anglian herring has altered since the early onset of maturity, and that the centres are now *larger than before*, the three's and four's being the same. How then can these herrings be predicted from the Bløden fish?

The next attempt by CUSHING and BURD to prove early maturity was by the calculation of the yearly recruitment since 1923, and here I have re-drawn their Figure II, 6 to illustrate a fallacy (Figure 1).

They have assumed that, taking the whole series of years 1923–55, full recruitment was not completed until the fish were *five* years old, the basis for

this assumption being Figure 1. For reasons which are not stated, they have grouped my pre-war distributions as 1924–27 and 1928–39, and "the age most abundantly represented is assumed to be that by which recruitment is complete." They point out that there has been a gradual shift of the most abundant age-group towards the younger ages, which, they say, is a "remarkable piece of evidence that a change in recruitment can take place." Nothing could be further from the truth. To begin with, there is very little difference in the average age distributions from 1928–51, the dominant age-group being the four-year-olds, and we know that there has been a change since 1951, but it is the 1924–27 series that is at fault in the diagram. This upper part of the figure represents the average of four early age distributions made by me on the East Anglian fishery, and although care was taken to cover the whole area with the sampling, the work in those days was purely exploratory, no attention being paid to weighting or other considerations.

The inadequacy of the data can be seen from my Figure 2 which gives the material on which the top part of Figure 1 is based. From these histograms it appears that the 1921 year-class (which proved later to be a very abundant one) was poorly represented in 1925 as four-year-old fish and it is that, together with the high percentage of fives in 1924 and 1926 which causes the peak in Figure 1 to be at five years. That this is due to bad sampling in the early days rather than to some change in maturity can be demonstrated from two outstanding facts: (1) the total number of fish examined during the East Anglian season of 1925 was only 510, or five samples, and (2) in the whole of my data from 1923 to 1955 there was only one year in which the four-year-olds appear to be less numerous than the fives of the following season. *That year was 1925.* It is obvious, therefore, that CUSHING and BURD's assumption on which their calculation was based is wrong, and therefore the resulting percentages of recruits in each year cannot be correct.

3. Mortality Rates

The very nature of the East Anglian herring fishery makes the estimation of mortality rates extremely doubtful except perhaps when they are calculated on a very broad basis. The fishing area resembles a coastal corridor through which the fish pass on their way south to the spawning grounds, but the shoals are not at all homogeneous. It is an established fact that the herrings migrate according to age, the younger ones coming first, thus the sixes and sevens of one year generally arrive earlier in the season than the sevens and eights of the following year. Again, years of sampling have taught us that the age composition of the shoals varies considerably in each week of the season, therefore those winds that affect "availability" can play havoc with calculations of "abundance", and in consequence, year-to-year mortality rates can vary enormously.

For these reasons, I have avoided such intimate calculations in a single year-class, but instead, have confined the estimation of mortality rates to all the fish older than five years and for an average period covering several years. CUSHING and BURD are aware of this danger of year-to-year estimations but they have used only the intervals 5/6 and 6/7 for the periods 1935–38, 1946–49, and 1950–55, which means that their mortality coefficients given in their

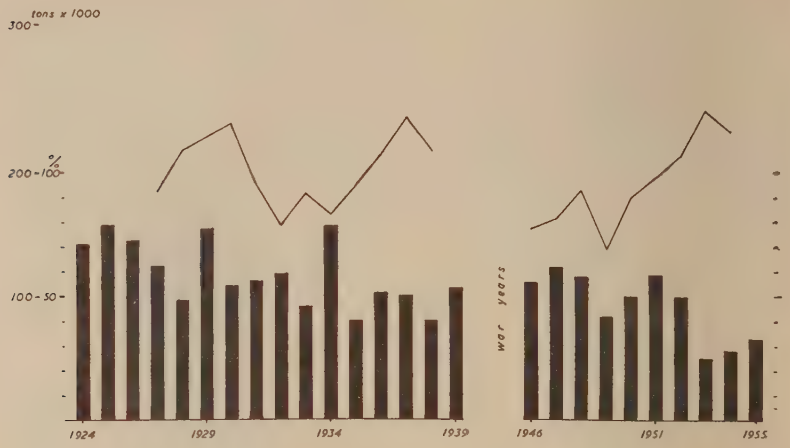

Figure 3.

Table 7 are the result of averaging three sets of very variable observations for 1935–38, three sets of equally variable ones for 1946–49, and five sets of similar quality for 1950–55. Their Table 7 is not very good evidence on which to base far-reaching conclusions, and the fact that in 1946–49 the coefficient for the ages 5/6 was 0·40 while that for the interval 6/7 was only 0·13 should at once suggest that the value of the calculations was suspect. Equally doubtful is their estimation of 0·81 for the ages 5/6 and 6/7 during 1952–55, this high rate being attributed to excessive trawling in the Channel after 1951. An examination of the data collected between 1952 and 1955 shows that during the interval 1953–54 the mortality rates for the adult fish were *well below average*, and also that immediately after the Channel trawling began, in 1951–52, the rates were equally low. These figures certainly do not furnish evidence of a dramatic change due to trawling.

Cushing and Burd have attempted to show that increases in total catch immediately before the war and again after 1950 were accompanied by high mortality rates, and they, together with Graham (*World Fishing*, Dec. 1956) have associated the increase in trawling in the Channel with the depletion of the adult stock and the consequent failure of the November fishing. In the first place, it is quite certain that whatever their calculations of mortality coefficients may show, there was no failure of the November fishing during the period 1935–38, from which we can conclude that the events of the two periods of high calculated mortality were not similar.

Graham's claim that the failure of the adults and the November fishing is due to excessive trawling is based on a table showing the total annual catch of herrings in the southern North Sea (see also Cushing and Burd, Table 1) and a diagram which compares this annual catch with the percentage of herrings aged five years and over, in the East Anglian drifter catches. In Figure 3, I have reproduced Graham's figure with one addition. I have added a column for the 1939 season at East Anglia. If this last column is covered up, the diagram gives the impression that just before the war, up to 1938 and again

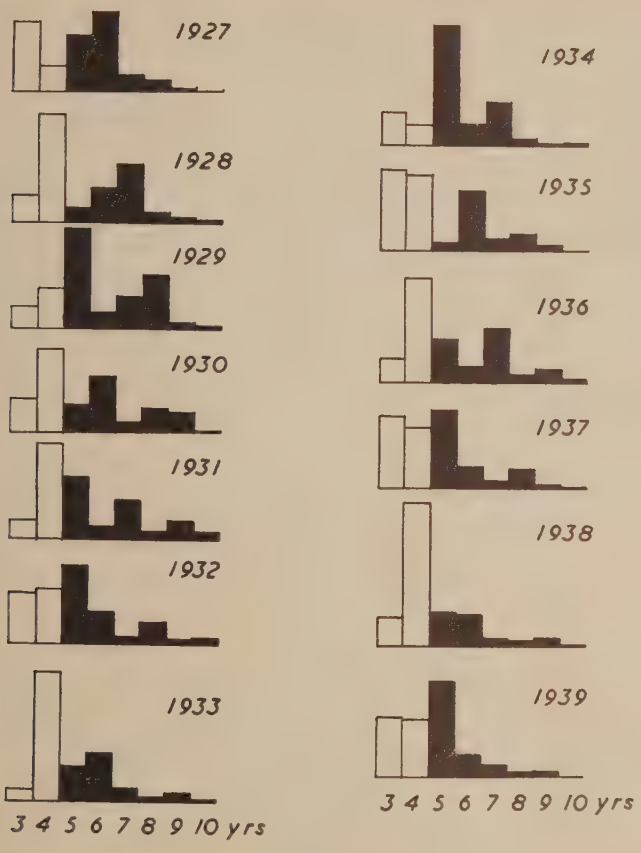

Figure 4.

after 1953 there were periods of high catches accompanied by low percentages of adult fish. Describing his own diagram, GRAHAM says that "there is an earlier period of lowered percentage of old fish in 1938 and 1939 and that too was a period of high total catch" . . . but he did not include the 1939 percentage in his figure. Had he done so, the illusion of the lowered "survival" of adults would have disappeared because *in 1939 the older fish were quite up to average quantities.*

Let us examine in detail the implications of GRAHAM's diagram. The period 1924–26 is one of high "survival" as shown by the height of the black columns, but the total catch is not given. There is good evidence that it must have been high in 1924 for about 200,000 tons were landed at Yarmouth and Lowestoft in that year by the East Anglian fleet alone. Then again, the 1929 period was one of high catch and high "survival" and, as I have already shown, the high catch of 1937–38 cannot be associated with anything but normal "survival". The high "survival" of 1934, on the other hand, occurs during a period of low

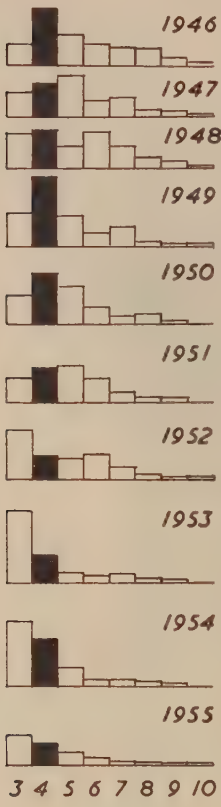

Figure 5.

total catch, so we have, before the war, one case in which low catch is associated with high "survival" but no case in which a high catch is accompanied by low "survival".

The post-war part of the diagram certainly gives the immediate impression of high catch coupled with low "survival", but closer examination shows that this association is not supported by the facts of the case. It must be remembered that each black column in the diagram does not represent a single biological unit but rather *six separate year-classes* all lumped together. Thus, if we consider a herring to be an adult after its fourth year, it follows that the five-year-old fish have been reduced in numbers by one year's fishing, the six-year-olds by two fishings, the sevens by three fishings, up to the ten-year-olds which have been affected by six separate fishing seasons. Each black column in Figure 3 shows, therefore, the total effect of six fishing seasons on what are called collectively the "adult fish" so how can we logically associate the total catch in any one year with the height of its corresponding column? The low column of 1953 is not connected with the high total catch of that year but rather with the catches of the six previous seasons *when the catches were very much lower*.

The "Total Catch" figures themselves are not very convincing either. The annual average total catch for the period 1935–38, one of the high periods, was 217,000 tons, and for the period of increased trawler activity in the southern North Sea, 1951–54, it was 223,000 tons. This represents an increase of rather less than 3 per cent. which by any standards cannot be called serious. CUSHING and BURD, discussing their Table 1, point out that during the period 1950–54 the total catch increased by 34 per cent. over the period 1946–49, but, while this is quite true, it gives a wrong impression of the seriousness of the trawlers' activity, because during the years immediately after the war the catching power of all the fishing fleets was very much reduced as a result of the war. It is a comparison between periods of full fleet activity that matters, and, so far as mortality rates are concerned, it matters not whether the herrings are caught by drifters or trawlers.

In Figure 4 I have drawn the percentage age composition of the East Anglian shoals for the years 1927 to 1939 inclusive, and the "adult" fish that correspond to the black columns in GRAHAM's diagram are shown also in black. This picture gives the true explanation of the changes in the percentage of old herrings at East Anglia from year to year and it is obvious that the governing factor is the fluctuation of the year-classes throughout the series. For example, 1929 has a high percentage of old fish because of the two very good year-classes of 1921 and 1924 which appear as eight-year-olds and five-year-olds respectively. Similarly, 1934 has a good showing of old herrings because of the rich 1927 and 1929 year-classes which are now seven and five years old.

The age-group which influences the height of GRAHAM's black columns most of all is, quite naturally, the five-year-old group, and when this group is poorly represented the number of "adults" is low.

The low value of the 1938 column which marked the end of GRAHAM's series in Figure 3 is clearly due to two things: (a) the low number of five-year-olds coming from the very bad year-class of 1933, plus the other very poor year-class of 1930 (three-year-olds in 1933), and (b) the high percentage of four's in 1938 which depressed all the other age-groups. It was this same abundant year-class of 1934 that was responsible for the revival of the adult fish in 1939 as shown in Figure 3, and GILIS, (Ann. Biol., 1946) has produced evidence that it was the mainstay of the "adults" for several years after 1939.

Figure 5 shows the age composition of the post-war herring shoals of the East Anglian fishery and as in the pre-war figure it will be seen that once again it is the lack of five-year-old fish after 1952 that is the main cause of the depletion of the "adult" stock, and, as this is the result of the change in recruitment it can in no way be associated with fishing after the fish leave the East Anglian grounds. Even if the rise in the mortality rate is admitted, it is surely unreasonable to place all the blame on the Channel trawling. Everything that happens to the fish between one November and the next must be taken into account, and it is quite likely that trawling to the north of East Anglia would have as important an effect as trawling to the south of the area.

Summary

According to some investigators there are two main causes of the East Anglian herring failure. These are (a) an advance in the age of first maturity which has the effect of bringing more three-year-olds into the commercial shoals, and (b) excessive trawling for adults on and near to the spawning grounds. A critical examination of the available data throws considerable doubt on the claim that, because there was an abundance of *Calanus* in 1950 the East Anglian three-year-olds increased their growth-rate and matured early. Differences in *average length* do not necessarily mean changes in *growth-rate*, and the changes in the length l_1 which have been associated with "early maturity" can equally well be used to prove interference with recruitment by the Industrial Fishery.

It has been claimed that the East Anglian data show that the pattern of recruitment has changed since the period 1924–27 but an examination of individual year-classes shows that there was no such change. The importance of calculated mortality rates is discussed and the data which couple the rise in these rates with trawling for adults in the Straits of Dover and Eastern Channel is examined critically. A study of year-class abundance is considered to be indispensable in dealing with the problem of the absence of adult fish and the fallacy of treating "adult fish" as a single biological group is pointed out. It is suggested that if the rise in the mortality rate is dependent on increased trawling for adults, then the trawling to the north of East Anglia should be considered as well as trawling to the south of the area.

Fat Cycles of North Sea Herring

By

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Introduction

During the past 50 years the fat content of the herring has been extensively studied by a number of workers, MILROY (1906, 1907, 1908), JOHNSTONE (1915, 1918, 1919, 1920), BRUCE (1924), CHANNON and EL SABY (1932), LOVERN and WOOD (1937), YUDANOVA (1939), LÜHMANN (1953), BRANDES and DIETRICH (1953), and HANSEN (1955). They have shown conclusively that the fat content of the herring is intimately connected with two factors, feeding and time of spawning.

During 1956 an examination was made of the fat content of the herring caught in the drift-net fisheries, which take place off the English east coast between May and December.

Method

Samples of herring were obtained regularly from North Shields fish market between May and September. They were bought direct from the previous night's catch and dispatched to the laboratory at Lowestoft iced in an insulated container. A few samples obtained at Whitby in September were transported in the same way. The samples obtained at Lowestoft from October onwards were all from the previous night's catch, except for a few of the later ones which had been iced for one night on board the drifter. After landing they were immediately transported from the fish market to the laboratory.

After the removal of two scales for age determination, the weight, length, sex, and stage of maturity of each fish was recorded. The gonads were then removed and weighed. If any quantity of food was present in the stomach, this was removed by cutting a slit in the stomach wall and squeezing the contents out, care being taken not to remove any of the mesenteric fat, which is often considerable during the summer months. The fat determinations were therefore made on herring which were complete except for gonads. In this way

Table 1

Variation of fat content with length

(Numbers of fish in parentheses)

	Virgin Herring		Mature Herring				
	Mean fat % Mat. st. I	Mean fat % Mat. st. I–III	Mean fat % Mat. st. III	Mean fat % Mat. st. IV	Mean fat % Mat. st. V	Mean fat % Mat. st. V	Mean fat % Mat. st. VI ♀ only
Length in cm.	June 16– Sept. 15	June 16– Sept. 15	June 10– Sept. 17	June 1– Sept. 30	June 16– Aug. 15	Oct. 15– Nov. 15	Dec. 18
21	20·8 (5)	20·5 (3)	20·7 (2)	–	–	–	–
22	16·2 (3)	21·6 (5)	24·1 (10)	19·1 (1)	–	–	12·4 (1)
23	20·3 (4)	22·0 (4)	22·4 (14)	21·2 (4)	–	19·0 (1)	10·4 (1)
24	20·1 (1)	22·5 (3)	24·4 (15)	20·6 (9)	20·7 (5)	17·6 (3)	14·1 (1)
25	29·8 (1)	23·4 (6)	23·7 (5)	20·1 (6)	22·0 (8)	17·5 (6)	11·5 (1)
26	–	21·8 (2)	21·9 (7)	22·1 (6)	19·4 (4)	17·6 (4)	6·4 (1)
27	–	21·8 (2)	21·3 (2)	19·4 (3)	20·7 (11)	17·8 (9)	12·7 (1)
28	–	–	–	22·4 (3)	19·9 (2)	19·7 (1)	10·5 (1)
29	–	–	–	–	18·5 (2)	11·8 (2)	10·1 (1)
30	–	–	–	–	15·6 (1)	10·0 (1)	–
31	–	–	–	–	–	16·9 (1)	–
32	–	–	–	–	–	13·6 (1)	–

Variation of fat content with age

Age in years	Mean fat % Mat. st. III June 10– Sept. 17	Mean fat % Mat. st. IV June 1– Sept. 30	Mean fat % Mat. st. V June 16– Aug. 15	Mean fat % Mat. st. V Oct. 15 Nov. 15	Mean fat % Mat. st. VI ♀ only Dec. 18
3	23·2 (44)	21·3 (19)	20·9 (12)	18·3 (5)	12·0 (3)
4	23·2 (11)	20·3 (13)	21·3 (16)	16·9 (10)	10·5 (3)
5	–	–	17·5 (3)	18·4 (6)	–
6	–	–	17·7 (1)	16·2 (4)	–
7	–	–	15·6 (1)	19·7 (1)	10·3 (2)
8	–	–	–	–	–
9	–	–	–	9·4 (2)	–
10	–	–	–	16·9 (1)	–

The periods shown above are those during which the fat level of the particular maturity stage was fairly constant.

the true fat reserve of the fish was determined, without being obscured by the heavy sexual products, especially during the later stages of maturity.

After the above procedure the herring was completely macerated and homogenized in a modern high-speed blender, similar to that tested by BRANDES and DIETRICH (1952). Replicate samples had a mean variation of only 0·1% in fat content (range 0·0 to 0·3%) and 0·2% in moisture content (range 0·0 to 0·4%). A weighed portion of approximately 14 g. was then dried for between 8 and 9 hours in a vacuum oven at 90°C. The moisture content was calculated after weighing the dried tissue, which was then carefully broken up into small pieces and extracted for 8 hours in a Soxhlet apparatus. The solvent used was Analar Petroleum Ether, boiling below 40°C. After extraction, the residue was dried in the oven to remove any ether and then weighed again. The loss of weight during extraction, i. e., weight of fat, was then expressed as a percentage of the original wet weight of tissue.

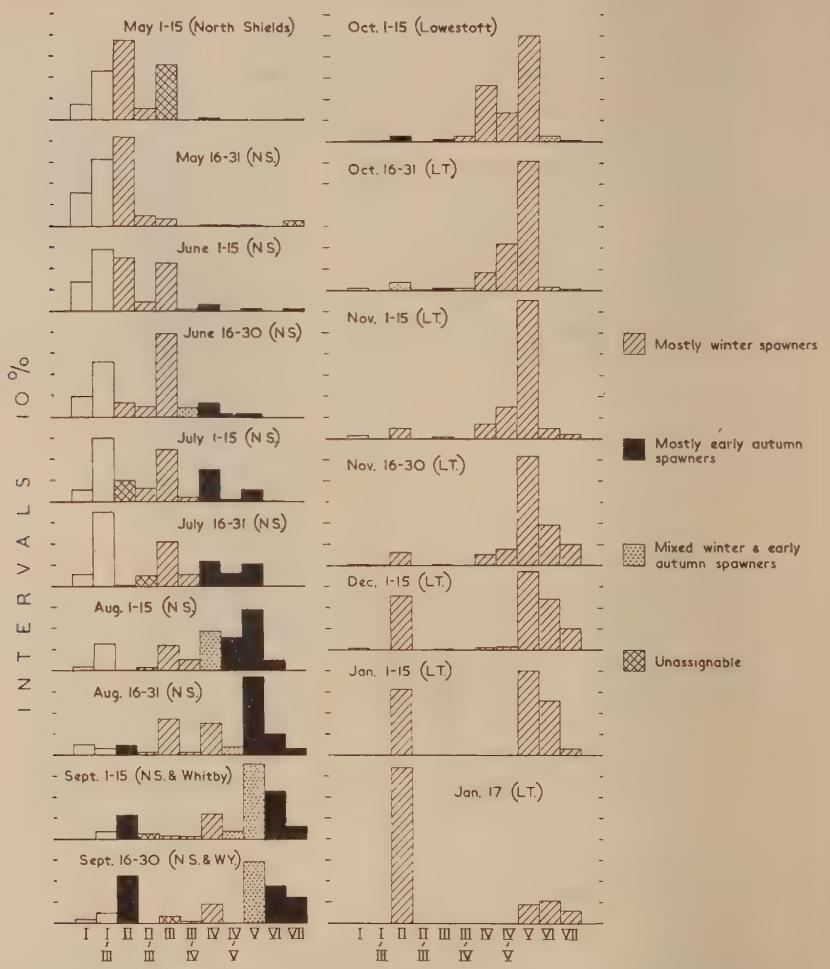

Figure 1. Distribution of maturity stages in laboratory samples of herring from North Shields, Whitby and Lowestoft, 1956/57.

The fat percentage calculated in this way was found to be on the average 0·2% higher (range 0·0 to 0·4%) than if calculated from the actual weight of fat recovered from the Soxhlet flasks. This was probably due to a small quantity of dried tissue being lost while it was being broken up preparatory to extraction, and during transference to the extraction tubes. Some loss of fat may also have occurred from the ether, during removal from flasks and subsequent evaporation.

In order to test the accuracy of the Soxhlet method, a quantity of residue was re-extracted using the hydrochloric acid digestion technique. Only a negligible quantity of fat was recovered, namely 0·01 g. of fat from an original 30 g. of wet tissue.

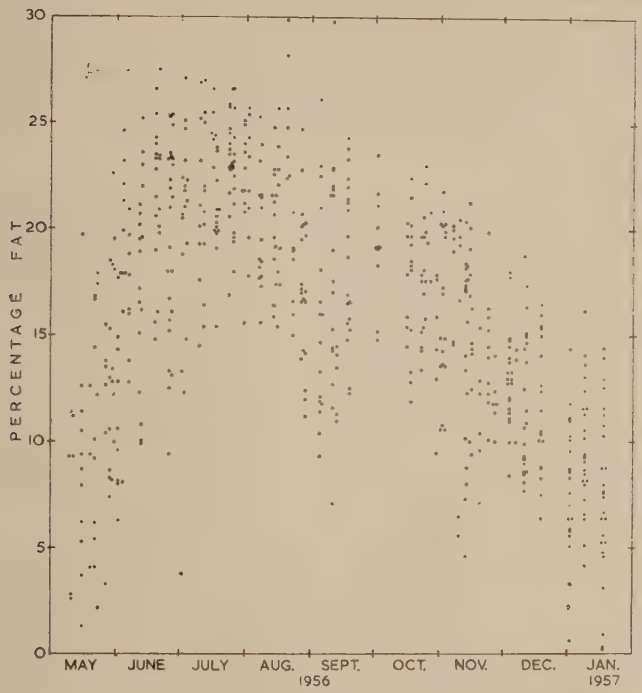

Figure 2. Fat content of the southern North Sea herring, 1956/57.

Variations of fat with maturity and age agreed with the results of other workers. There was no significant variation with age in the mature herring, up to at least 7 years of age. But, at maturity stage V there was a trend to lower fat values with increasing length, as if the demand on the fat reserves is greater at this time in the larger and more fecund fish. On the other hand there was a trend to higher fat values with increasing length in the virgin herring at maturity stage I–III, i. e., with gonads showing signs of developing for the first time, although this was not apparent in the case of the virgin herring still at maturity stage I.

Results

In Figure 1 the maturity stages of all the herring examined in laboratory samples from North Shields, Whitby, and Lowestoft, during the period May 1956 to January 1957, are plotted as mean percentages for each half month. They fall roughly into two groups, those which spawn in late summer and early autumn and those which spawn in winter. Some stages cannot be assigned readily to either group, as for example spring spawners or mixed autumn and winter spawners. The virgin herring at maturity stages I and I–III have also not been included in the grouping.

In Figure 2, the fat content of each herring examined has been plotted against time. The marked variations occurring between May 1956 and January 1957

Table 2

Mean fat percentage by half-month periods at each maturity stage
(Numbers of fish examined in parentheses)

Date 1956 to 1957	Maturity stage I	I–III	II	II–III	III	III–IV
May 1–15	10·4 (2)	11·1 (3)	4·7 (6)	11·2 (1)	10·5 (3)	–
16–31	15·1 (7)	12·6 (3)	10·5 (7)	7·6 (4)	13·9 (5)	–
June 1–15	17·0 (5)	18·1 (4)	12·6 (10)	16·5 (2)	16·4 (8)	–
16–30	18·5 (3)	22·9 (4)	17·2 (7)	14·8 (1)	23·3 (9)	22·8 (6)
July 1–15	18·5 (2)	22·8 (5)	17·6 (1)	–	23·6 (12)	21·8 (4)
16–31	19·7 (3)	19·9 (4)	–	23·4 (10)	23·8 (6)	23·5 (1)
Aug. 1–15	21·2 (2)	22·2 (7)	–	21·6 (2)	22·5 (10)	23·9 (1)
16–31	19·9 (3)	20·7 (1)	–	–	25·3 (7)	24·8 (1)
Sept. 1–15	29·8 (1)	22·8 (4)	–	16·0 (1)	22·7 (4)	–
16–30	–	–	–	22·3 (2)	21·7 (4)	21·5 (2)
Oct. 1–15	–	–	–	–	–	20·3 (3)
16–31	19·8 (4)	–	–	18·5 (2)	17·6 (2)	20·5 (2)
Nov. 1–15	19·8 (6)	–	–	18·7 (3)	19·0 (5)	17·6 (1)
16–30	–	–	–	–	–	–
Dec. 1–15	15·1 (3)	–	–	–	16·2 (2)	18·0 (1)
16–31	16·0 (1)	–	–	–	–	–
Jan. 1–15	–	–	–	–	–	–
17	13·5 (2)	–	–	–	–	–

	IV	IV–V	V	V–VI & VI	VII	II
May 1–15	9·2 (2)	–	–	–	–	–
16–31	14·4 (2)	21·0 (2)	–	–	9·9 (3)	–
June 1–15	20·7 (9)	18·2 (3)	15·9 (3)	–	12·3 (1)	–
16–30	20·8 (4)	18·6 (4)	20·4 (4)	–	–	–
July 1–15	22·3 (4)	21·9 (2)	20·9 (8)	3·8 (1)	–	*12·8 (2)
16–31	21·3 (5)	23·3 (5)	20·9 (13)	–	–	–
Aug. 1–15	18·7 (3)	17·7 (3)	19·4 (8)	19·0 (8)	–	–
16–31	21·0 (3)	16·0 (1)	17·9 (7)	15·0 (5)	13·9 (3)	15·8 (4)
Sept. 1–15	20·3 (2)	14·2 (2)	14·5 (9)	13·9 (6)	13·3 (5)	11·2 (3)
16–30	21·6 (2)	–	15·8 (4)	–	15·7 (2)	13·9 (3)
Oct. 1–15	19·8 (3)	18·9 (4)	17·0 (5)	15·2 (1)	–	–
16–31	19·8 (3)	23·0 (1)	18·3 (12)	13·0 (4)	14·6 (2)	13·9 (6)
Nov. 1–15	19·6 (3)	18·7 (5)	15·8 (14)	12·0 (9)	9·1 (7)	14·6 (7)
16–30	–	–	14·6 (10)	11·9 (5)	11·4 (5)	10·0 (2)
Dec. 1–15	–	–	12·6 (15)	10·3 (11)	12·4 (6)	12·9 (7)
16–31	–	16·5 (1)	15·4 (2)	10·3 (11)	11·6 (2)	10·1 (1)
Jan. 1–15	–	–	10·0 (10)	8·9 (19)	5·5 (7)	9·4 (8)
17	–	–	11·2 (4)	5·7 (6)	4·1 (7)	8·8 (7)

* summer spawners

Note: Herring at maturity stage II are given in two columns above, in order to distinguish the fish at this stage during the early part of the Shields fishery, which have probably been spent for some considerable time, from the newly spent fish later in the year, following on from stage VII.

can be more easily explained if a comparison is made with the maturity data in Figure 1.

The fat content of the herring caught at the start of the North Shields fishery early in May 1956 was fairly low, after the winter months when little food is available. The majority of the herring caught at that time were virgins of maturity stages I and I–III, and mature recovering spents at maturity stage II.

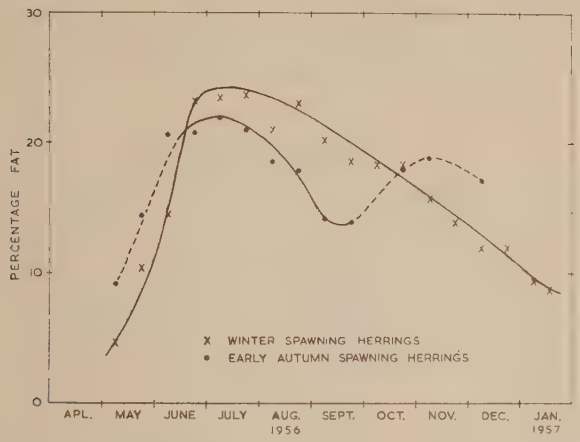

Figure 3. Fat cycles of the early autumn and winter spawning herring, 1956/57.

There then followed a period of intensive feeding for several weeks during which the fat reserve was rapidly built up and maturation of the gonads commenced.

By July a very high fat level had been reached, while fish which had been recovering spents in May had advanced in maturity to at least stage III, as also had a proportion of the virgin herring which had been at stage I–III at that time. From June onwards increasing numbers of herring at more advanced stages of maturity (i. e., IV and V) appeared in the catches. These spawned during August and September between the Yorkshire coast and the Dogger Bank. The fat content of many, both spawning stage VI and spent stages VII and II, was relatively low; hence the "tongue" of low values coming down in Figure 2 during the latter part of August and September. The winter spawning fish which were less advanced in maturity, i. e., those at stages I–III and III to IV in July, gradually developed until they had reached stages IV to V by the start of the East Anglian fishery in October. During the whole of this period there was a steady decline in fat content, which continued until sampling ended on 17. January 1957.

The winter spawning fish started to spawn in November, and once again the lowest fat values shown in Figure 2 during November to January occurred in the spawning and spent herring. By the middle of January spawning was virtually completed and fat content had again reached a low level.

In Table 2 are given the mean fat percentages of all the herring examined, at each stage of maturity, in each half month. From a combination of this fat data with the maturity data in Figure 1, the fat cycles of the two groups of maturing fish have been estimated. These are plotted in Figure 3, the points taken being set out in Table 3 below. The virgin herring at maturity stages I and I–III have not been included.

In Figure 3, the fat cycle of the early autumn spawners has been shown by a dotted line during May to June and again from September to December. This is because the small numbers of fish caught maturing in the early part of the Shields fishery, and as recovering spents in the East Anglian fishery, may

Table 3

Winter spawning herring 1956/1957

Date	Estimated mean fat content %	Main maturity stages Mean % fat content of each stage in parentheses
May 1–15	4·7	II (4·7)
16–31	10·5	II (10·5)
June 1–15	14·5	II (12·6) and III (16·4)
16–30	23·3	III (23·3)
July 1–15	23·6	III (23·6)
16–31	23·8	III (23·8)
Aug. 1–15	21·0	III (22·5) and IV (18·7)
16–31	23·1	III (25·3) and IV (21·0)
Sept. 1–15	20·3	IV (20·3)
16–30	18·7	IV (21·6) and V (15·8)
Oct. 1–15	18·4	IV (19·8) and V (17·0)
16–31	18·4	V (18·3) and IV–V (18·8?)
Nov. 1–15	15·8	V (15·8)
16–30	14·0	V (14·6) and VI (11·9)
Dec. 1–15	12·0	V (12·6) II (12·9) and VI (10·3)
16–31	12·0	V (15·4) II (10·1) and VI (10·3)
Jan. 1–15	9·4	V (10·0) II (9·4) and VI (8·9)
17	8·8	II (8·8)

Early Autumn spawning herring 1956

Date	Estimated mean fat content %	Main maturity stages Mean % fat content of each stage in parentheses
May 1–15	9·2	IV? (9·2)
16–31	14·4	IV? (14·4)
June 1–15	20·7	IV (20·7)
16–30	20·8	IV (20·8)
July 1–15	22·0	IV (22·3) and V (20·9)
16–31	21·0	IV (21·3) and V (20·9)
Aug. 1–15	18·6	IV–V (17·7) and V (19·4)
16–31	17·9	V (17·9)
Sept. 1–15	14·2	V (14·5) and VI (13·9)
16–30	13·9	II (13·9) and VI (?)
Oct. 1–15	–	–
16–31	18·0	II–III (18·5) and III (17·6)
Nov. 1–15	18·8	II–III (18·7) and III (19·0)
16–30	–	–
Dec. 1–15	17·1	III (16·2) and III–IV (18.0)

not be representative of the stock as a whole. However this may be, there is undoubtedly:—

(1) A build-up of the fat reserves in spring, in both groups, although in the early autumn spawners this probably occurs somewhat earlier.

(2) A secondary build-up of fat in the early autumn spawners after spawning, which follows with renewed feeding (Brandes and Dietrich, 1953).

The early autumn spawners are therefore in a much better condition to face the lean winter months when little food is available, than the winter spawners which are forced to subsist on their remaining reserve of fat during the rest

of the winter after spawning. Consequently the fat content of the early autumn spawners is appreciably higher than that of the winter spawners in the spring when food again becomes available.

Discussion

By maturity stages it is possible to make a separation of the herring caught in the drift-net fisheries off the English east coast, into two groups, i. e., early autumn spawners and winter spawners.

HANSEN (1955) examined the food and fat content of the virgin herring caught on the Bløden ground and was able to follow the fat cycle of these fish, which is effected only by feeding, during the greater part of the year. The fat cycle of the winter spawners, shown in Figure 3, is very similar to the fat cycle of the Bløden herring.

The fat cycle of the early autumn spawners, on the other hand, is considerably modified due to the fact that the period of cessation of feeding prior to spawning, and the period of recovery after spawning when feeding again takes place, both occur during the summer and autumn when food is still relatively abundant.

The early autumn spawners have a considerable advantage over the winter spawners when the plankton outburst occurs in the spring, because:—

(1) They have a higher fat content to start with.

(2) They are probably in the feeding area and able to take immediate advantage of the marked increase in food, some 4 to 5 weeks earlier than the winter spawners, which do not enter the feeding area until the end of April.

This advantage which the early autumn spawners have over the winter spawners during the crucial spring feeding period, fixes the separate fat cycles of the two groups.

It is probable that the two groups of herring described here as early autumn spawners and winter spawners, are in fact the Bank and Downs stocks of herring, and this illustrates their physiological separation.

Summary

The fat content of herring caught in the drift-net fisheries off the English east coast during 1956/57 has been examined. Herring from mainly two stocks, i. e., Bank and Downs, are caught in these fisheries and the fat cycle of each stock has been estimated.

In both stocks there is a rapid build-up of fat in the spring. The fat content of the Downs herring, after reaching a maximum in July, steadily declines over the rest of the year as the gonads mature. When spawning has been completed by about mid-January, the fat content of the Downs stock has reached a low level. The remainder of the fat reserve is then largely used up during the rest of the winter, when little food is available. There is a marked decline in the fat content of the Bank herring prior to spawning, which takes place during the latter half of August and September, but after spawning, with renewed feeding, a secondary rise in fat content occurs. This enables the Bank herring to pass the winter with an appreciably higher fat content than the Downs herring, which are unable to replenish their reserve of fat for several months after spawning.

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Seasonal Fluctuations in the Catches of Salmon in the Baltic

By

Gunnar Alm

I. Introduction

The yield of a particular fish species depends first and foremost on the size of its aggregations which occur in various localities in the course of its spawning and feeding migrations. This is, of course, particularly true of a species so markedly migratory as the salmon. The Baltic area must, on the whole, be considered a fairly uniform and enclosed area as regards the propagation and migration of salmon. Hence, an investigation of the salmon fishery in this area should undoubtedly be of interest, as it may serve as a contribution to our knowledge of salmon migrations in general and, at the same time, furnish some practical information about the methods used in the fishery and the regulations proposed.

Previous investigations of the salmon fishery and of the distribution of age-groups of salmon in the Baltic area have been made (Alm, 1919, 1924, 1934, 1954; Dixon, 1931; Hessle, 1923; Järvi, 1938, 1948; Rosén, 1918), and salmon marking experiments have been carried out on a large scale, particularly by the Swedish Migratory Fish Committee (Alm, 1941, 1943; Carlin, 1953, 1955, 1957). The information so obtained, together with the fishermen's experience, have quite naturally furnished interesting information about the fishing seasons. It appeared that a more systematic survey of the salmon fishing seasons as they appeared in various records would most likely contribute further toward an elucidation of these questions, and accordingly such a survey was made and is described in the following pages; the catches in different months and different years are reviewed and whenever the data at hand permit it, the variations in the size of the salmon are also studied.

II. Material

Information about the size of the salmon catch in different months is obtainable from the literature in regard to Denmark (the Danish *Fiskeri-Beretning*, 1952–55) and West Germany (Kändler, 1955) as well as to both of the two southernmost Swedish provinces, Blekinge and Skåne (official Swedish statistics, *Fiske*). Further, valuable information on West German, Danish, and Polish conditions has been given by Professor Kändler, Mr. Knudsen, and Dr. Chrzan, respectively. Similar information is not available

Figure 1. The location of the most important fishing ports with fish marketing associations (●); the largest salmon rivers and the location of the lightships (◎).

Table 1

Weight of salmon caught in the Baltic (tons)

	1951	1952	1953	1954	1955
Sweden, Baltic coast					
Norrbotten County	185	162	79	62	56
Västerbotten C.	42	36	21	21	17
Västernorrl. C.....	59	60	37	23	27
Gävleborg C.	43	72	12	14	17
Uppsala C.	1	–	–	–	–
Stockholm C.	31	22	32	28	17
Södermanl. C.....	5	6	2	3	–
Östergötl. C.....	9	6	5	11	2
Kalmar C.....	119	57	23	27	9
Gothland C.	206	153	81	119	48
Blekinge C.....	351	194	115	158	96
Kristianst. C.	15	15	9	15	5
Malmöhus C.	11	8	6	3	2
Total	1,077	791	422	484	296
Finland, Baltic*)	352	383	347	?	?
Denmark, Baltic.....	1,096	1,350	753	962	609
West Germany, Baltic*)..	136	144	75	121	157
Poland, Baltic.....	82	43	24	43	17
Total Baltic.....	2,743	2,711	1,621	–	–
Sweden, Baltic rivers.....	210	226	170	130	111

*) Sea trout occasionally included.

from East Germany and the USSR whereas, through the kindness of Professor Halme, some data for Finland have been obtained from the Board of Agriculture's Bureau for Fishery Investigations. My sincere thanks are due to the above-mentioned gentlemen.

In the case of the Swedish salmon fishery, information about the monthly catches and to a certain extent also about the size distribution of the salmon was collected with the kind co-operation of some of the Fish Marketing Associations operating along the east coast of Sweden. These associations, as well as some of the county fishery officials and others interested in the fishery, have provided me with much material of great value, and I hereby express my gratitude for the readiness with which this material was furnished. Figure 1 shows the regions covered by the associations from which information was obtained. The areas from which the various associations obtain their supplies will be described later. This primary material, covering the 5-year period 1951–1955 (in some cases even longer) and including years of good as well as poor catches, is kept at the Institute of Freshwater Research at Drottningholm.

With respect to the material as a whole, it should be mentioned that in the case of Germany, Denmark, Skåne-Blekinge, and Gothland practically the whole catch is included. In other cases, part of the catch has been disposed of privately. However, the bulk of the catch, and at any rate a proportion large enough to be considered representative of the particular season, was handled by the associations. For the double purpose of avoiding direct publication of the information provided by the Fish Marketing Associations and ensuring a uniform treatment of the data, the figures on the distribution of the catch in different months and in size-groups are expressed as percentages. These are

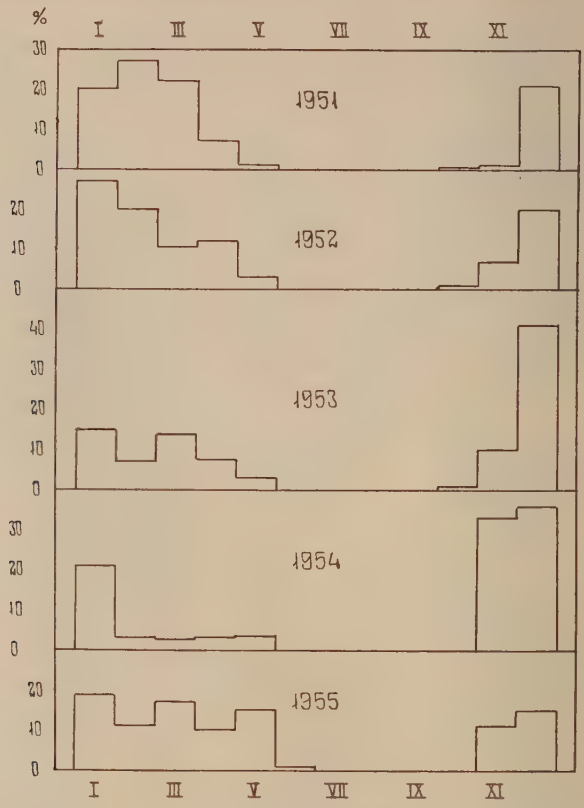

Figure 2. West Germany. The monthly catches expressed as percentages of the annual catch.

shown in the form of graphs or tables. To save space, it was judged advisable to omit from the text the tables from which the graphs were prepared. To permit a comparison of the yield in different years, Table 1 gives figures for the salmon catches in the different areas treated below.

III. Monthly Distribution of the Salmon Catch and the Size of the Salmon in Different Areas in Different Years

In this section, the monthly distribution of the salmon catch and its changing pattern from year to year are studied; the areas involved are dealt with in geographical order, from south to north. The distribution of the size-groups in different months is also discussed, in so far as information is available. The variations in the fishing seasons in different areas and the reasons therefore are dealt with in a later section.

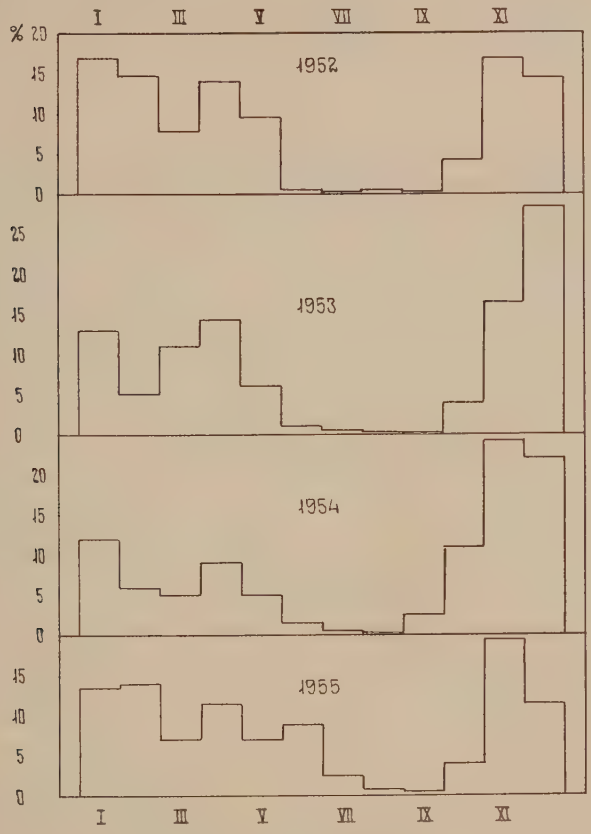

Figure 3. Denmark. The monthly catches expressed as percentages of the annual catch.

West Germany

The West German salmon fishery is conducted almost entirely in the south-eastern parts of the Baltic; in spring drift-nets are mostly used, but during the remainder of the year drift-lines are employed. The monthly distribution (Fig. 2) varies a little from one year to another. The main catch is taken in the period December–January, and salmon fishing is suspended in summer and early autumn. In 1951 the catch was exceptionally heavy in February–March, in 1954 a fairly good catch had already been taken by November, and in 1955 the spring fishery was continued with fair success until some time in May.

The salmon caught have decreased in size. According to KÄNDLER (1955), salmon weighing less than 2 kg. constituted 5% of the total salmon caught in November–December 1950, while salmon weighing more than 8 kg. constituted 24%. In 1953, the corresponding figures were 26 and 7%, respectively. In

1954 the proportion of small salmon weighing less than 2 kg. was 13% of the total catch and only 4% were more than 8 kg. A calculation by weight would, of course, have rendered different figures.

Denmark

The Danish salmon fishery in the Baltic has grown very much during the last ten years. Formerly only fishermen from Bornholm and other places along the Danish Baltic coast participated in the fishery, concentrating mainly on the southern parts of the Baltic, but the fishery now attracts numbers of fishing vessels from North Seeland and Jutland. These large vessels enable Danish fishermen to operate throughout the year and their activities have been extended to cover most of the Baltic proper and in some cases even parts of the Gulf of Bothnia and the Gulf of Finland. The bulk of the catch is taken with drift-lines, though in summer drift-nets are also employed. The latter gear is, incidentally, most commonly used in spring in the waters around Bornholm and in the south-eastern part of the Baltic.

Figure 3 shows that the Danish fishery takes place in a longer period than the German. The catch is, however, usually poor in July and August, the actual summer months, but fishing in winter and spring often yields heavy catches, though ice may be a hindrance. Towards autumn the catch increases steeply and usually reaches its peak in November. As with the German fishery, in 1955 good catches were made in late spring and early summer. Thus, 17% of the total catch of that year was taken in June, in which month usually only very few salmon are caught. The autumn fishery commenced exceptionally early in 1954. It has not been possible to obtain information about size distribution in the catches in different seasons.

Poland

The yields of the Polish salmon fishery in the period 1951–55 was rather small (Table 1), following very large catches in the years 1946–50. The fishery is conducted only in the parts of the Baltic adjacent to Poland. Both nets and hooks are employed. The monthly catch distribution is shown in Figure 4. In earlier years the main catch was taken in spring, but fairly big catches were also obtained in late autumn. In other years, especially 1949, the autumn landings have been the best. The catches in the depth of winter are mostly rather poor, and no salmon at all are caught in the summer months, July–September.

East Germany and the Baltic countries

With respect to the salmon fishery conducted by East Germany and the Soviets, the information obtained suggests that the fishery has become of minor importance in recent years. Fishermen from these countries nowadays concentrate primarily on cod and other species which provide more meat than the salmon.

MIEZIS (1936), however, gives figures for the seasonal catches of salmon and sea trout in the years 1924–34 on the Latvian coasts, partly the open Baltic coast and partly the Gulf of Riga. The salmon fishery in the Baltic

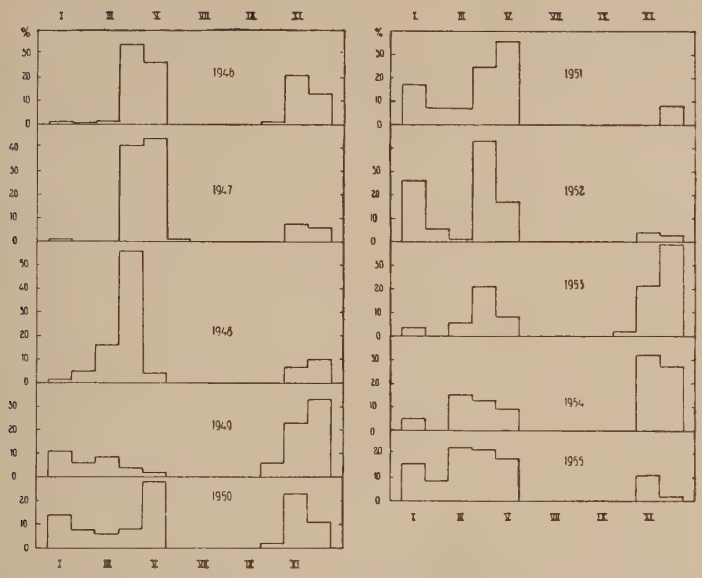

Figure 4. Poland. The monthly catches expressed as percentages of the annual catch.

only amounted to about 10% of the total catch. Fairly small quantities of sea trout are included in the figures. The catches for these years are shown (as percentages) in Figure 15. The figures for the Baltic somewhat resemble the figures for Blekinge, though with better catches in spring. The figures for the Gulf of Riga show that the main fishery is concentrated in the summer and early autumn months.

Sweden: Blekinge and Skåne

Records for the monthly landings of salmon in Blekinge and Skåne (those at the latter, however, being negligible [see Table 1]) date back to 1946; they are illustrated in Figure 5. The fishery is carried on by drift-nets in the south-eastern part of the Baltic in spring largely. At other seasons both fixed lines and drift-lines are employed in various areas in the southern part of the Baltic and closer to the coasts of Blekinge and Skåne, in Hanö Bay. In these regions nets are also commonly used. In Blekinge a good many salmon are caught by trolling.

Figure 5 shows that the spring fishery is the most important and yields the largest catches. This is particularly true of the months April–May. In some years, (1949 in particular) the autumn fishery was also fairly satisfactory, though it is usually distributed more evenly over several months. During summer the catches are poor, which is also the case in the actual winter months. The year 1947 is noteworthy because of the marked concentration of catches in the month of May.

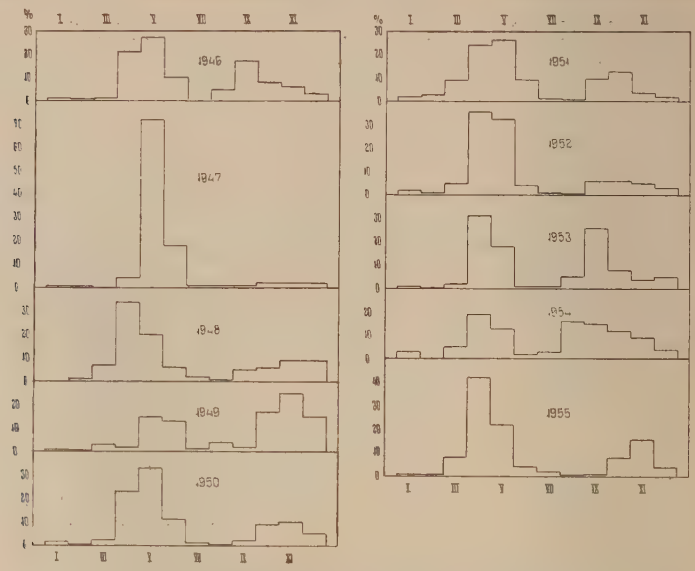

Figure 5. Sweden: Blekinge and Skåne. The monthly catches expressed as percentages of the annual catch.

As was also pointed out in the case of the German landings the size of the salmon caught has decreased. Table 2 shows that in 1951 salmon weighing more than 8 kg. constituted 29% by number and 41% by weight of salmon caught that year, while only about 1% by both number and weight consisted of salmon weighing less than 3 kg. The corresponding figures for 1954 were 10 and 25%, respectively, for the larger salmon, and for the smaller salmon, 19% by weight and as much as 47% by number. In 1955, the proportion of small salmon had again declined to 6% by weight and 17% by number.

Figure 6, which is based on information provided by the Central Association of Fishermen in Blekinge, illustrates the average distribution of size-groups in each month during the last three years. The figure shows that the proportion of small salmon weighing less than 3 kg. was largest in late summer and early autumn and was sometimes as much as 36% by weight and 66% by number of the total catch. Large salmon weighing more than 8 kg. were relatively common in the catches in April–May and especially in November–December.

Sweden: Gothland

After Blekinge, the province of Gothland has the most important of the Swedish salmon fisheries. From very early times, salmon have been fished by both fixed lines and drift-nets, chiefly in the local waters both westward and eastward of Gothland. In the course of the last ten years fishing operations have been extended further afield, in particular to the south-eastern part of the Baltic. At the same time, fishing with drift-lines has become increasingly popular and this method of fishing plays a much more important rôle in the Gothland fishery than in the Blekinge.

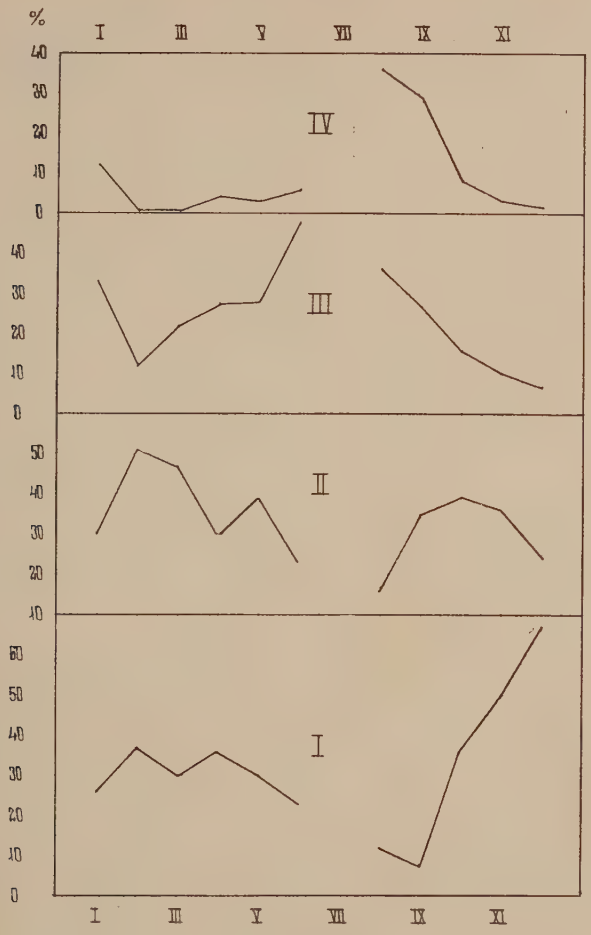

Figure 6. Blekinge. Percentage of different size-groups by weight in the same months. (I = 8 kg. >, II = 6–8 kg., III = 3–6 kg., IV = < 3 kg.). Averages for the period 1953 1955.

Table 2

Blekinge. Percentage of different size-groups by weight and number in different years

	Weight				Number			
	> 8 kg.	6–8 kg.	3–6 kg.	< 3 kg.	8 kg.	6–8 kg.	3–6 kg.	3 kg.
1951	41	36	22	1	29	34	36	1
1952	51	33	15	1	37	36	26	1
1953	51	29	14	6	31	25	19	25
1954	25	27	29	19	10	16	27	47
1955	37	30	27	6	21	24	38	17
1951–55	45	32	20	3	26	29	33	12

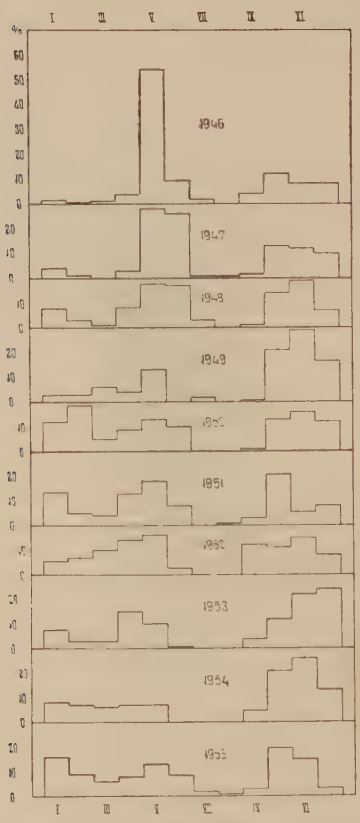

Figure 7. Sweden: Gothland. The monthly catches as percentages of the annual catch.

In the case of Gothland also, information on fishing seasons is available for a 10-year period (Fig. 7). The first point to command attention is that in the early years of the period the bulk of the catch was taken during spring — in one single month in 1946. In some years, the autumn catches were the largest, and this was usually the case in the latter part of the period. This was especially pronounced in 1949, as at Blekinge. This trend is undoubtedly attributable in part to the change-over to drift-lines, which is the most advantageous method of fishing in autumn. Before this change-over the best catches were taken with drift-nets in spring. It should be added that the largest salmon are caught in spring. The catch curves are, incidentally, very similar to those for Blekinge, especially in regard to the insignificance of the summer catch. Winter fishing yields more here, however, than at Blekinge.

As in other regions previously mentioned, the size of the salmon shows a downward trend in this area. Table 3 gives the percentages of the 4 size-groups in the last 5-year period. In 1951, the largest and the smallest size-group constituted 37 and 7%, respectively, of the catch by weight and 23 and 18%, respectively, by number. In the 1954 landings, which in both Germany and Blekinge were noteworthy for the large proportion of the smallest size-group, this group amounted to no less than 25% by weight and 48% by number of salmon landed in Gothland. In 1955, however, the distribution of size-groups was closer to normal. In this context it should be mentioned that during the period 1946–50, before the widespread use of drift-lines specifically designed for small salmon, salmon weighing less than 3 kg. constituted only some 3% of the total annual catch by weight and 10% by number.

Figure 8 shows the average percentage by weight and number of the size-groups described above in each month of the period 1951–55. The curves leave no doubt about the fact that large salmon were predominant in spring and early summer, whereas small salmon were very scarce then. The smaller size-groups are of most importance in autumn and winter. The differences between the conditions in Gothland and Blekinge are dealt with later in this paper (p. 423).

Table 3

Gothland. Percentage of different size-groups by weight and number in different years

	Weight			
	> 8 kg.	6–8 kg.	3–6 kg.	< 3 kg.
1951	37	32	24	7
1952	41	28	23	8
1953	35	28	21	16
1954	20	25	30	25
1955	30	30	28	12
1951–55	34	29	25	12
1946–50	56	28	13	3
	Number			
1951	23	27	32	18
1952	26	22	31	21
1953	18	19	25	38
1954	8	13	31	48
1955	15	21	35	29
1951–55	18	21	31	30
1946–50	40	29	21	10

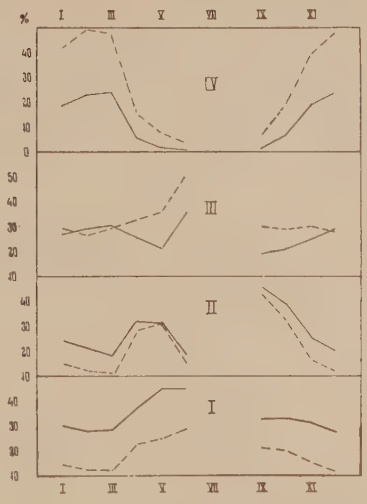

Figure 8. Gothland. Percentage of different size-groups by weight and by number in the same months (I = 8 kg. >, II = 6–8 kg., III = 3–6 kg., IV = < 3 kg.). Averages for the period 1951–1955.

Sweden: the coast from Kalmar County to Stockholm County

In the Baltic counties south of the Åland Sea, which are now to be discussed, salmon fishing is of less importance than in the two provinces previously mentioned. For this reason the records of catches in the years for which information has been obtained have been amalgamated, so that Figure 9 gives only the average catch for each of the four counties. The figures on which the curves are based also include sea trout which, unfortunately, are not separately recorded by the marketing associations. However, the catch of sea trout is almost negligible, except in the vicinity of the mouth of the river Emån.

As regards Kalmar County, which has the most important fishery of the southern group, salmon are fished with drift-nets off the coast as well as in the waters around Öland and Gothland and to some extent also in the southern part of the Baltic. In recent years drift-lines have come into use. Two associations have provided information about the Kalmar fishery. In both cases the records go to prove that the bulk of the catch is taken in spring and autumn while there is almost no fishing in late summer and early spring. No information is available about the distribution of size-groups.

The distribution of the catch over the year is very uniform in the case of Östergötland, Södermanland, and Stockholm Counties. In these three districts, salmon are fished with nets during spring and with fixed lines and drift-lines in autumn. Fishing is normally carried on in the inshore waters, in the neighbourhood of Häradsskär, between Hävringe and Landsort, and along the coast of outer Södertörn and the whole of the Uppland coast, but also at some distance off shore. A number of fishermen operate on the grounds around

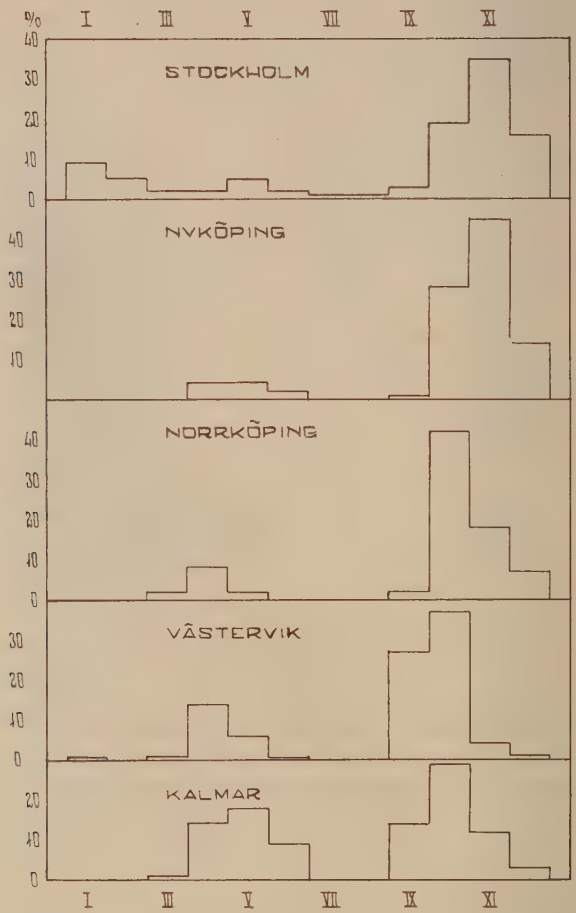

Figure 9. Sweden: the coast from Kalmar County to Stockholm County. The average monthly catches expressed as percentages of the annual catch.

Gothland, on the Midsjö Banks, and even in the south-eastern parts of the Baltic. Some fishermen, most of them from Stockholm County, regularly visit the last-named fishing grounds, particularly in spring, to fish with drift-nets. These activities are reflected in the curves of all of these three counties, though no large catches are taken at that time of year. In the northern part of Stockholm County, however, the spring fishery may sometimes yield fairly well. The main catch, however, is usually taken in autumn. The maximum catch is taken in October in Östergötland County, and in November in the other two counties, though fairly good catches are taken in October and December also. During summer the catch is negligible.

No details are available of the size of the salmon landed in these counties. According to information provided by the marketing associations the landings in spring and early autumn consist chiefly of large salmon. As the year advances, size shows a downward trend and by the end of December the smaller salmon are predominant. In the southern part of Stockholm County the autumn fishing in 1954 yielded an exceptionally large proportion of salmon weighing between 2 and 3 kg.

Sweden: the coast from the Åland Sea to Kvarken (= the Bothnian Sea)

In these districts the summer salmon fishery is mostly carried on with large traps or other similar stationary gear and is therefore located close inshore. In addition, ever since the 'forties, a very important and profitable fishery has been operated in autumn and early winter with fixed lines at sea, often at a distance rather far from shore. Some of the types of salmon lines used for this purpose are furnished with eight to ten hooks instead of the usual one or two. Several experiments have been made with drift-lines, but results were negative and this tackle is now rarely employed. The association in Gävle handles some salmon from the Uppland coast, but the major part of their supplies originates from the Hälsingland coast. The bulk of the salmon caught off Medelpad is handled by the Sundsvall association, while the Härnösand association deals with the catch taken by Ångermanland fishermen.

The data provided by these three associations are very uniform. Thus, Figure 10 shows that almost every year the catch curves exhibit two maxima, one in summer (June–July) and another in autumn; catches often remain fairly good until the very end of the year. In winter fishing is brought to a standstill by the ice. In the southernmost part of the district fishing may sometimes be resumed as early as March; it rarely begins in the Sundsvall district before April, and in the northernmost part of the region fishing is not in full swing until May. The graph also shows that in all three areas the largest catches in the autumn fishery of 1955 were taken later than usual, the peak in these years occurring in November as compared with October in other years. As regards the Sundsvall area the 1952 and 1953 seasons are distinguished from other seasons by the merging of the two peaks.

In the above-mentioned districts, and also further north, small salmon and sea trout are not recorded separately but are, for statistical purposes, entered under the common title of "trout". Consequently, there are only three size-groups of salmon, the smallest comprising those weighing between 3 and 6 kg. It is therefore impossible to obtain data respecting the occurrence of salmon proper weighing less than 3 kg. As regards the other three size-groups, Table 4 gives the percentage by weight of each group in different years. Although, for this reason, the figures in the table are not directly comparable with those relating to Gothland and Blekinge, large salmon tend to be more markedly predominant in these waters than in the Baltic. Apart from a few exceptions, the figures for the three areas agree fairly well. In all the three areas, the 1954 catch contained an unusually high proportion of large salmon, at the expense of the middle group, while no increase in the volume of the smallest group was recorded. In this connexion it should be borne in mind that the high proportion of small salmon recorded as present in the Baltic that year applied to salmon weighing less than 3 kg.

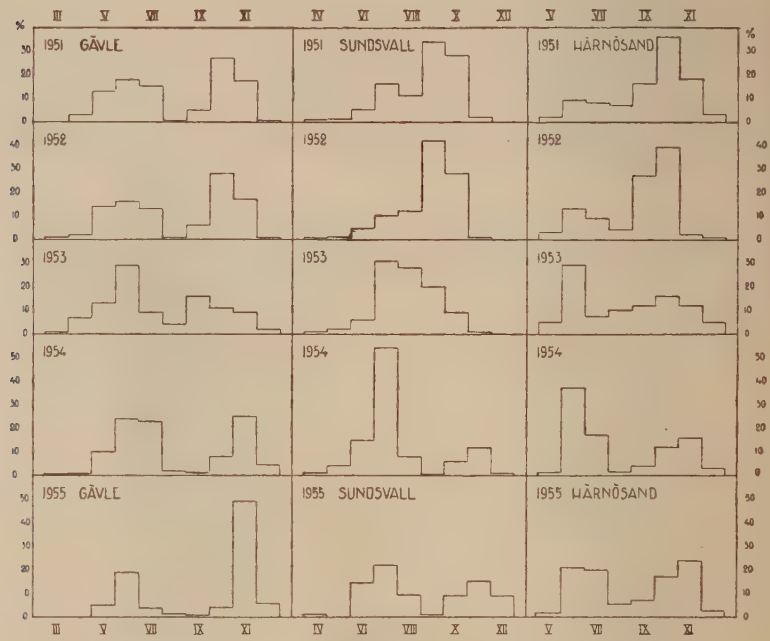

Figure 10. Sweden: the Bothnian Sea. The monthly catches expressed as percentages of the annual catch.

Table 4

The Bothnian Sea. Percentage of different size-groups by weight in different years

	> 8 kg.			6–8 kg.			3–6 kg.		
	Gävle	Sundsv.	Härn.	Gävle	Sundsv.	Härn.	Gävle	Sundsv.	Härn.
1951	52	55	57	22	20	21	26	25	22
1952	56	32	46	22	25	27	22	43	27
1953	51	56	58	23	21	24	26	23	18
1954	62	68	70	13	9	13	25	23	17
1955	59	55	58	23	24	18	18	21	24
1951–55 ...	54	48	54	22	21	23	24	31	23

The distribution of the size-groups in different months is illustrated in Figure 11. In all three areas large salmon predominate at the time of the summer peak, while smaller fish are common in the large catches which are taken in autumn. In late autumn, the percentage of small salmon again decreases while that of large salmon rises. The curve showing the proportion of medium-sized salmon to a certain extent resembles that relating to small salmon, though the fluctuations from month to month are less marked.

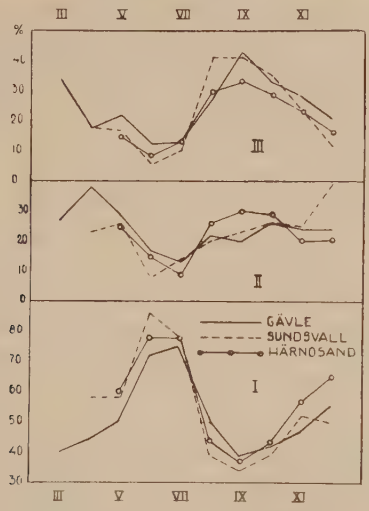

Figure 11. The Bothnian Sea. Percentage of different size-groups by weight in the same months (I = 8 kg. >, II = 6–8 kg., III = 3–6 kg.). Averages for the period 1951–1955.

Sweden: the coast from Kvarken (Umeå, Nordmaling) to Haparanda (= the Gulf of Bothnia)

In the localities immediately south of Kvarken and everywhere further north in the Gulf of Bothnia salmon are successfully fished with large traps. Formerly nets were also employed but nowadays these are not commonly used. Trials have been made with hook and line, but the results were disappointing. The districts under consideration get their fish from the grounds between Holmöarna and Nordmaling to the south and the northernmost parts of the Gulf of Bothnia to the north (cf. Fig. 1) and their records agree almost perfectly with one another with regard to the fishing seasons (Fig. 12). The pattern followed by these landings, however, differs in some essential respects from that prevailing in the Bothnian Sea. In all districts which draw their supplies from the Gulf of Bothnia the catch curve exhibits only a single, very conspicuous peak; in the southernmost district this occurs in June, but farther north it is more evenly spread over June and July. This pattern remains, on the whole, unchanged from one year to another. In the Kalix and Nikkala localities the year 1953 differs from normal, however, in exhibiting a marked concentration of the catch in the month of June. A tendency for the fishery to occur earlier that year is also recorded for the other regions in the Gulf of Bothnia. In addition to the substantial summer catch a small quantity of salmon is taken in autumn. This is particularly the case in the Ume area where fishing is continued until some time in November; in this locality a slight upward trend in the catch curve is noticeable. In the northernmost areas fishing ceases in August–September or the beginning of October.

Some of the associations have provided data on the catch of salmon weighing less than 3 kg., which, as stated above, are combined with sea trout. This

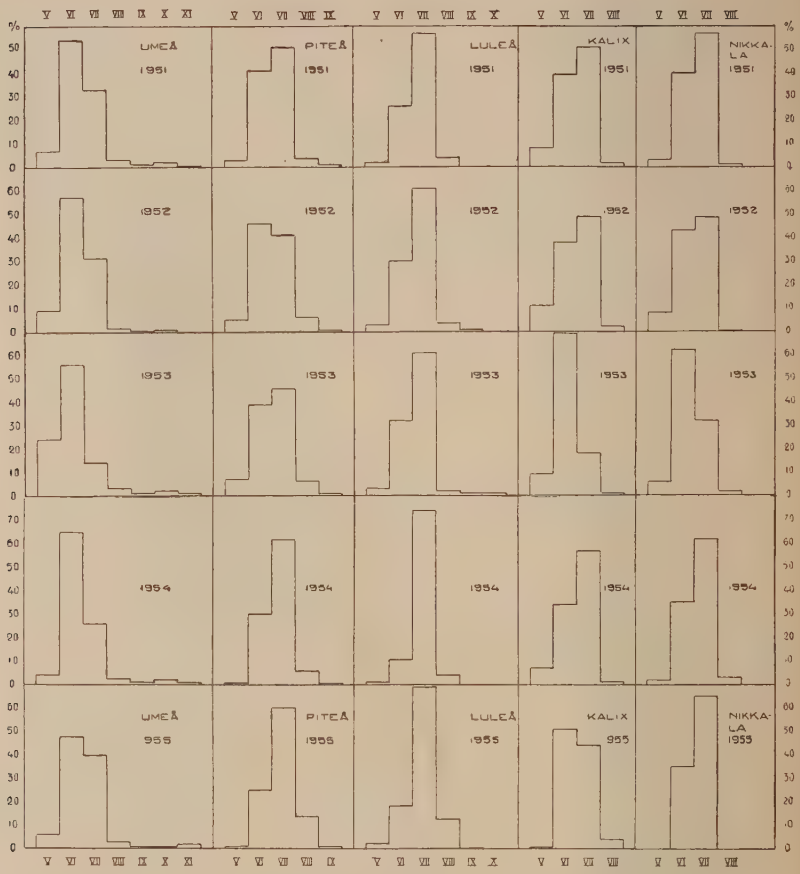

Figure 12. Sweden: the Gulf of Bothnia. Monthly catches expressed as percentages of the annual catch.

Table 5

Gulf of Bothnia. Percentage of different size-groups by weight in different years

	> 8 kg.		5–8 kg.		3–5 kg.	
	Piteå	Luleå	Piteå	Luleå	Piteå	Luleå
1951	65	74	23	18	12	7
1952	63	76	26	18	10	7
1953	67	73	22	21	11	6
1954	73	78	20	20	8	7
1955	65	74	23	18	12	7
1951–55	66	75	23	18	11	7

information bears out the view that within this group salmon predominates from the end of June to the end of August, while in September and later in autumn sea trout by far outweigh salmon. The average monthly distribution of these catches in recent years, expressed as percentages, is given in the table below.

	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Piteå	11	40	31	12	6	–	–	–	%
Luleå	6	51	23	8	4	6	1	1	%
Kalix	20	49	21	2	2	6	–	–	%

The catches are evidently heaviest in June–July, when they consist chiefly of salmon, whereas they are much smaller in autumn when they contain fewer salmon. Hence it appears that in these northern areas salmon weighing less than 3 kg. are mostly taken in summer.

Information about the size-group distribution is available only for Piteå, Luleå, and, to some extent, Kalix. Table 5 shows that salmon weighing more than 8 kg. are commoner in these localities than in the Bothnian Sea. According to the data provided by the associations, the smallest size-group comprises salmon weighing between 3 and 5 kg., while further south the smallest group comprised salmon between 3 and 6 kg. Accordingly, a lower proportion of the smallest group ought to be present in the catch in the Gulf of Bothnia. Throughout the period under review the proportion of this group in the Luleå district was no more than 7%, which seems to suggest that such salmon are even scarcer here than in the Bothnian Sea. There are no appreciable variations from one year to another. Information on size-groups is available for 1950, and it is noteworthy that even in that year, when catches were abundant, the percentages of the different groups remained almost unchanged at 68, 22, and 10%, respectively, for the Piteå district and 76, 18, and 6%, respectively, for Luleå. In Kalix, where only salmon weighing more than 8 kg. are recorded separately, this group constituted 70% of the total catch over the 5-year period. It may also be mentioned that in August 1954, the catch of small salmon and sea trout amounted to as much as 18% at Piteå and 13% at Luleå as compared with the normal percentage of 12 and 8, respectively. Thus, in 1954 the total catch of this size-group was exceptionally large in August, in which month the bulk of the catch consists of salmon. It would therefore seem likely that the catch of salmon less than 3 kg. was larger that year than usual.

The size-group distributions in the few months in which fishing is carried on are shown in Figure 13. In June and July, the two months in which the bulk of the catch is taken, the distributions are almost identical. In this case, too, it is apparent that the salmon weighing between 3 and 5 kg. constitute a small proportion of the catch. This group predominates only in August, when the catches are insignificant. Further, at both Piteå and Luleå the largest salmon, weighing more than 8 kg., form a larger part of the catch in July than in June. This is, incidentally, also the case at Kalix, where the proportion of salmon weighing more than 8 kg. is 68% in June and 72% in July. Hence, there is perfect correspondence between these three areas as regards size distribution.

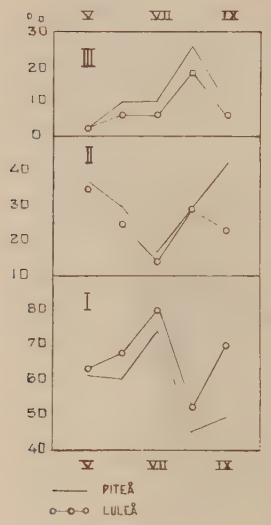

Figure 13.

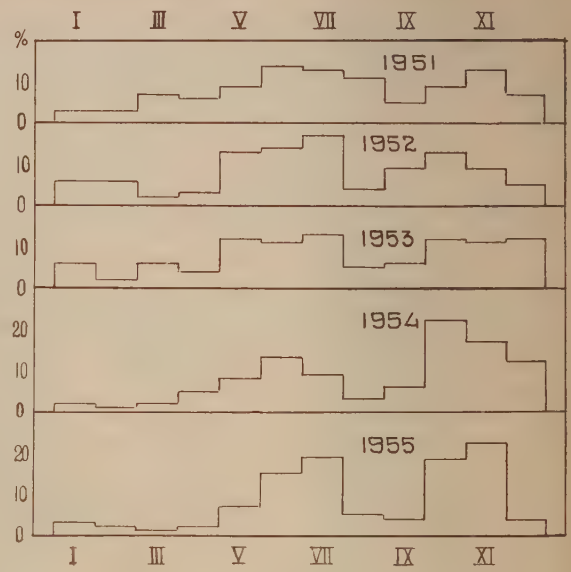

Figure 14.

Figure 13. The Gulf of Bothnia. Percentages of different size-groups by weight in the same months (I = 8 kg. >, II = 5–8 kg., III = 3–5 kg.). Averages for the period 1951–1955.

Figure 14. Finland. Monthly landings of salmon in Helsingfors expressed as percentages of the annual catch.

Finland

In respect of Finland, no information on the monthly catch of salmon is available, nor have any statistics been published in recent years. Data are available, however, for 1953 and are given separately for various coastal districts (LIEDES, 1955). As mentioned above, records of monthly landings of salmon in Helsingfors have been kept during the last five years (Fig. 14). It seems, however, that this survey includes only part of the very rich catches of salmon taken in summer in the northernmost part of the Gulf of Bothnia, as most of these fish are salted and stored for marketing later on. Finnish salmon fishing in the Gulf of Bothnia is carried on almost exclusively by means of traps in early summer; in the Finnish fishery in the Bothnian Sea, like the Swedish, both traps and hooks are used and the fishing season covers the autumn; off southern Finland and in the Gulf of Finland fishing is mostly by fixed lines or drift-lines, and is carried on chiefly in spring (May) and autumn. Only a few fishermen, mainly from Åland, fish for salmon in the Baltic proper.

The largest catches, some 40% of the total landings, originate from the grounds between the Swedish border and a little south of Uleåborg, from the northern coasts of the Bothnian Sea, and from Åland; almost 30% come from the Gulf of Finland.

The curve exhibits two peaks, one in summer and the other in autumn. They are evidently connected with the trap fishery carried on in the Gulf of Bothnia

at the height of summer and with the hook-and-line fishery in the Bothnian Sea, the Gulf of Finland, and, to a lesser degree, the Baltic, which takes place in autumn. If the catch from the Gulf of Bothnia had been included in the figures, those for the months of May–July would have been appreciably higher.

IV. General Review of the Causes of the Fluctuations in the Monthly Salmon Catch

It has been shown in the preceding paragraphs that the seasonal courses of the salmon catches vary considerably from one place to another in the Baltic. At the same time, it has been shown that in general the seasonal pattern remains fairly constant from year to year. Hence it is justifiable to regard the values obtained as characteristic of the localities concerned. The average values for the entire period are embodied in Table 6. To enable the several fishing seasons to be compared, these values have been plotted and curves drawn through the points (Fig. 15). By considering these curves, and bearing in mind the present state of knowledge of the salmon's biology and the results obtained from salmon marking experiments (particularly the recent ones) I have attempted in the following pages to assess the causes of the local variations in the fishing seasons.

Investigations into the age, particularly the smolt age, of salmon caught in different parts of the Baltic have proved (*op. cit.*, p. 399) that during their sea life most of the salmon originating from rivers in northern Sweden and Finland usually remain in the Baltic proper, very often in the southern and south-eastern parts. Furthermore, it has been shown that most salmon remain in the sea for a full 3-year period while others spend two or two-and-a-half, and sometimes one-and-a-half or four, years in the sea before they first ascend to the spawning grounds.

This is confirmed by salmon marking experiments; these also teach us certain facts about the various types of salmon migration. The charts made by Carlin (1957) which show the positions of recapture of marked salmon in different months provide us with the following information. The smolts released in spring in the rivers Indalsälven and Ångermanälven were recaptured in the following summer at various places in northern waters. It was not until late autumn of the same year and the succeeding winter that they were found in the Baltic proper around Gothland and farther to the south-east; in late winter and in spring some were recovered from the Danish Sounds and, exceptionally, in the Kattegat. At the height of summer, after a year's sojourn in the sea, a few fish were recaptured in the Bothnian Sea, particularly in the waters close to the rivers in which they were marked; some were retaken on their way up the river. Between the beginning of September and the end of the year, i. e., after the salmon had spent two summers in the sea, recaptures again became numerous off both Swedish and Finnish coasts and all over the Baltic and Bothnian Sea. During the winter and the following spring recaptures were almost more common towards the southern and south-eastern parts of the Baltic. Later on, in the third summer, in June–August, several recaptures of marked salmon were received from the southern part of the Bothnian Sea and from various rivers; recaptures in the Baltic were rarely made in the hottest season, but in August and, particularly, September, however, after the third

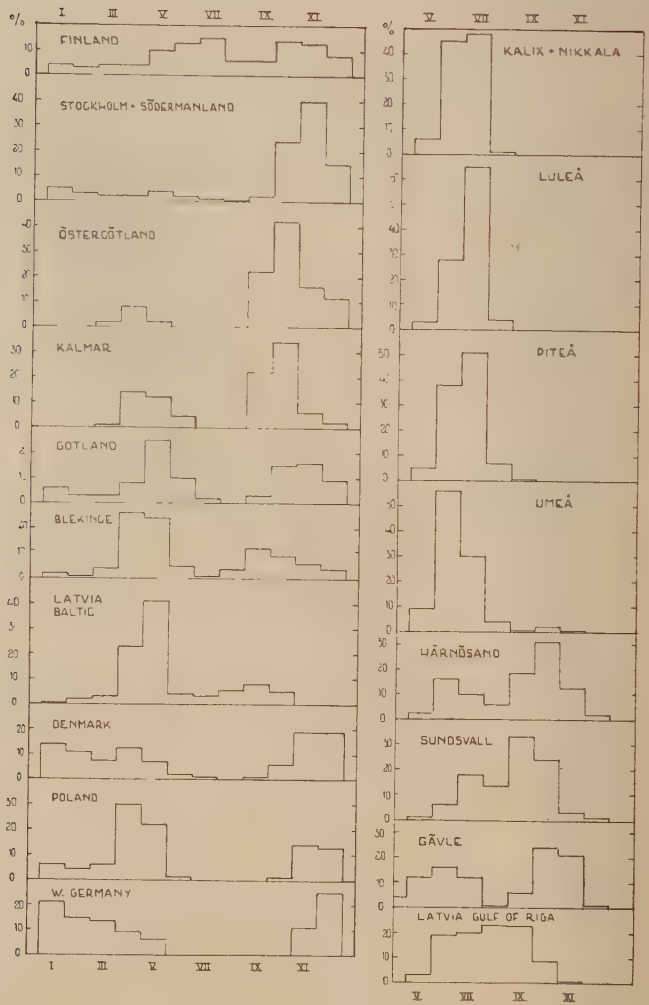

Figure 15. Average monthly catches of salmon expressed as percentages of the annual catch.

Table 6

The monthly salmon catches in different regions expressed as percentages of the annual catches. The figures are averages for the periods indicated

Month	W. Germany 1951–55	Poland 1946–55	Latvia 1924–34		Denmark 1952–55	Sweden				
			Baltic	Gulf of Riga		Blekinge + Skåne, Karlskr. 1946–55	Gotland Visby 1946–55	Kalmar 1949–55	Västervik 1952–55	Östergötl. Norrköping 1948–55
I	20·8	6·5	0·4	0·1	14·1	1·7	6·6	–	0·4	–
II	14·6	3·9	1·8	0·1	10·6	0·7	3·5	–	0·1	–
III	13·6	6·7	3·1	0·2	7·7	4·5	2·9	0·6	0·6	1·8
IV	8·7	30·3	23·2	0·8	12·3	26·6	7·2	13·7	13·3	8·0
V	5·8	22·5	41·4	3·0	7·3	24·5	25·5	18·2	5·9	1·5
VI	0·1	0·3	4·6	19·5	2·2	5·4	9·9	8·8	0·1	–
VII	–	–	3·6	20·5	0·6	1·1	1·1	–	–	–
VIII			7·1	23·5	0·2	4·2	0·1	–	–	–
IX	–	–	8·4	22·9	0·9	11·7	3·3	14·1	27·2	21·9
X	0·1	1·6	6·0	8·7	6·0	9·5	14·9	29·0	47·9	42·0
XI	11·8	14·6	0·0	0·7	19·2	6·1	15·2	12·4	3·9	17·7
XII	24·5	13·5	0·4	0·0	18·9	4·0	9·8	3·2	0·5	7·1

Month	Sweden										Finland 1951–55
	Södermanl. Nyköping 1946–50	Stockholm 1949–55	Gävle 1951–55	Sundsvall 1951–55	Härnösand 1951–55	Umeå 1951–55	Piteå 1951–55	Luleå 1951–55	Kalix 1951–55	Nikkala 1951–55	
I	1·0	9·2	–	–	0·8	–	–	–	–	–	4·2
II	0·5	4·5	–	–	–	–	–	–	–	–	2·9
III	0·5	2·1	0·2	–	–	–	–	–	–	–	3·9
IV	4·0	2·2	2·6	0·2	–	–	–	–	–	–	3·9
V	4·0	5·1	12·4	1·5	2·5	9·0	3·8	2·4	8·1	3·3	10·1
VI	1·8	1·8	16·6	6·3	16·1	56·3	38·3	27·5	45·4	43·2	13·4
VII	–	0·6	12·1	17·9	10·1	30·1	50·8	65·3	44·7	52·9	14·0
VIII	–	0·5	1·5	13·8	6·1	2·6	6·7	4·6	1·7	0·6	6·2
IX	1·0	3·1	7·1	32·5	18·2	0·3	0·4	0·2	0·1	–	6·3
X	28·0	19·3	24·4	24·4	31·3	1·1	–	–	–	–	13·9
XI	45·1	35·3	21·6	3·1	12·5	0·6	–	–	–	–	13·4
XII	14·3	16·3	1·5	0·3	2·4	–	–	–	–	–	7·8

summer at sea, recaptures in the Baltic were common. During the succeeding winter, when the salmon had spent three summers and two winters at sea, recaptures became markedly concentrated in the south-eastern parts of the Baltic; this was especially so in late winter and spring, and lasted until sometime in May. By the fourth summer the number of recaptures in the Baltic had again fallen sharply, and a large number of marked salmon were caught in the Bothnian Sea and in the rivers. Much the same trend appears in the results of the smolt marking experiments in the river Luleälv in May 1954 (CARLIN and JOHANSSON, 1957), though in this case recaptures in the northern waters were confined almost exclusively to the Gulf of Bothnia and the Lule River, only one salmon being recaptured in the Bothnian Sea.

Reference may also be made to the extensive marking experiments made both recently and several years ago with salmon which had already spawned naturally or which were used for egg taking and artificial spawning; in others small salmon caught in the sea were marked. These experiments also furnished interesting information on salmon migration; they proved that after their first spawning a comparatively large number of salmon return to the Baltic, where they are caught.

From salmon marking experiments and other biological investigations it has been learnt that the length and weight of the salmon at different stages of their sea life are roughly as follows:—

	Length, cm.	Weight, kg.
After 1 summer and 1 winter in the sea	30– 40	0·3– 0·5
– 2 summers – 1 – – – –	50– 60	1·2– 2·5
– 2 – – 2 – – – –	65– 70	2·5– 4·0
– 3 – – 2 – – – –	75– 80	4·5– 6·0
– 3 – – 3 – – – –	85–100	7·0–12·0

In the following sections it will be demonstrated that the facts stated above can be brought into harmony with the variations in the fishing seasons and the size-group distributions.

The Baltic

As regards the Baltic proper, the first point to notice is that the results of the marking experiments bear out the view that the salmon fishery in this region is very poor when summer is at its height. Fishermen in various countries are of the opinion that this must be attributed to the fact that in hot weather the salmon favour deeper water and avoid the southernmost parts of the Baltic. It is therefore reasonable to expect some correlation between landings and water temperature. These latter are illustrated in Figure 16, which give curves of the monthly mean temperature of the surface water as ascertained from observations carried out on board lightships since the early 'twenties. These data were compiled by KOCZY (1953). The curves show that the water temperature prevailing from spring to late autumn at Falsterbo, which may be presumed to represent the conditions prevailing in the southern parts of the Baltic, is one or more degrees higher than that recorded on the Öland Reef, and a comparison with records from "Svenska Björn", south of Åland, shows an even greater difference.

It has already been mentioned that the German and Polish salmon fisheries, carried on in the southern part of the Baltic, are suspended during the period

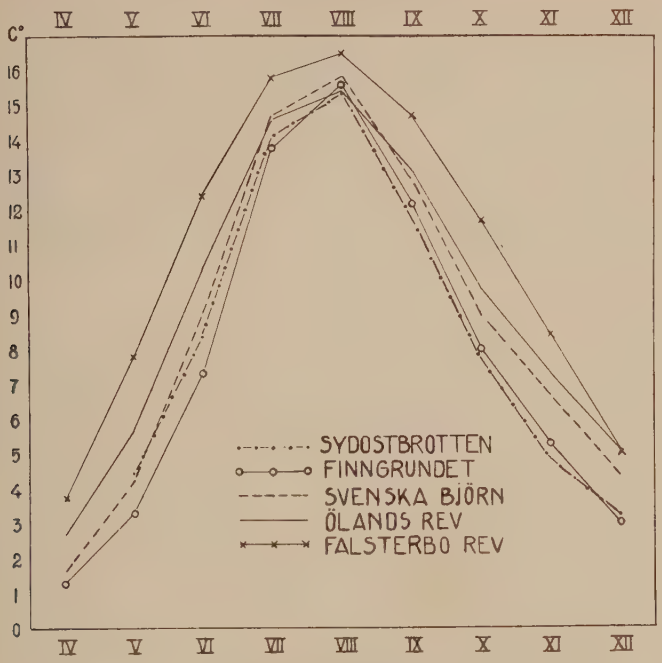

Figure 16. Monthly mean temperature of the surface water at Swedish lightships.

June–October. The mean temperature at "Falsterbo Rev" is 12·5°C. in June and 11·7° in October. In May and November the values are 7·8° and 8·4°, respectively. On the other hand, the Danish fishery and the Blekinge and Skåne fisheries, which extend over large areas of the Baltic, are successfully continued into June and, at any rate as regards the last-named fisheries, into September and October also. In June the mean water temperature is 10·3° on the "Ölands Rev" and 8·9° at "Svenska Björn"; the corresponding values in July are 14·7° and 14·6°, respectively. In September the temperature decreases to 13·2° at the "Ölands Rev" and 13·1° at "Svenska Björn", and in October to 9·8° and 9·0°, respectively. With these figures in mind, it would seem likely that in spring or early summer, when the water temperature at the surface has risen to upwards of 10·0°, and may reach 11°–12°, the salmon seek the deeper water layers. It is beyond the scope of this paper to discuss whether this is due solely to the increase in temperature or to the possibility that such fish as the Baltic herring, small cod, and sand-eel, on which the salmon principally feed, seek deeper water. If that were so it would then be reasonable to expect that the salmon would seek deeper water at an earlier date in the southern part of the Baltic than in the central parts; this would conform with the annual courses of the fishing season. Towards autumn, when the temperature again decreases to about 10°, the salmon return to the upper water layers. In the northern and central parts of the Baltic this return occurs in September–October, but not until October–November in the southern part, fishing operations being resumed accordingly.

Table 7

Surface water temperature at Swedish lightships

		"Falsterbo Rev"	"Hävringe*)"	"Svenska Björn"
September:	Mean.....	14·7	13·2	13·1
	1954.....	14·2	11·2	12·7
October:	Mean.....	11·7	9·2	9·0
	1954.....	10·1	6·7	8·2
May:	Mean.....	7·8	5·9	4·2
	1955.....	6·3	4·0	3·1
June:	Mean.....	12·4	10·6	8·9
	1955.....	11·1	9·0	7·2

*) Observations at "Hävringe" began in 1952.

It was stated on pp. 403 and 404 that the German and Danish salmon fisheries commenced unusually early in the late summer of 1954 and continued an unusual length of time into the early summer of 1955. Thus, in 1954, 32·8% of the German catch was taken in November as compared with an average of 10·4%, and in May 1955, 24·4% was taken, as compared with an average of 7·5%. Danish fishermen took 11% of the 1954 catch in October, the average for that month being 6%, and in June 1955, the catch amounted to 9% as compared with an average of 3%. This must be ascribed to the fact that in the autumn of 1954 the salmon moved from the deep water to the upper layers earlier than usual and in the spring of 1955 they remained in the upper water layers longer than usual, for similar reasons. Table 7, which gives the temperatures at certain Swedish lightships, shows that in both autumn 1954 and spring 1955 the water temperature was in general 1°–2° below normal. The autumn cooling of the water in the Baltic thus began earlier than usual in 1954 and the spring warming was unusually delayed in 1955. There is therefore every indication of an association between water temperature and the behaviour of the salmon.

It has not been possible, however, to establish a definite correlation between water temperature and catch of salmon in different years. This is but natural, considering the wide variety of factors which influence the salmon fishery. Among these factors may be mentioned weather conditions and the seaworthiness of the fishing vessels, persistent winds and currents, which cause the salmon to favour different places in the Baltic, the predominance of particular size-groups in the catch, and so on. It is most probable that factors like these were responsible for the marked concentration of salmon catches into a single month, as occurred in Gothland County in 1946 and in Blekinge County in 1947.

Irrespective of such influences, it is evident, however, that during their sea life in the Baltic the salmon avoid the upper water layers in summer when the surface temperature is relatively high, and spend that season in deep water. This fact helps to explain the long suspension of the German and Polish salmon fisheries and the poverty of the Danish catches at the height of summer. The same explanation applies, although to a lesser degree, to the Blekinge and Gothland fisheries and to other fisheries in the Baltic also.

In recent years several attempts have been made to catch salmon at the height of summer, mainly by angling in fairly deep water. This procedure is said to be extremely complicated and time-wasting, however. Lines and spreaders

get antangled and when cod are abundant, as they sometimes are, they immediately rise to the bait and prevent the salmon from taking it. Some Danish fishermen have recently tried fishing for salmon in deep water with drift-nets as well as lines. In the northern parts of the Baltic fairly good catches were taken, but in the southern parts of the Baltic results were less satisfactory. The difficulties connected with salmon fishing at this time of year may also be ascribed to the fact that at the height of summer the salmon favour a depth of 15–20 m., which, according to the lightship observations, is the depth at which the thermocline occurs. At this time of year the temperature of the upper water layer is approximately the same from the surface to the thermocline.

It has already been pointed out that whereas German and Danish fishermen take their heaviest catches in winter, these conditions do not apply either to the Blekinge and Gothland or the Polish fisheries, which overlap the German and Danish to some extent. The results of the marking experiments described above, (CARLIN, 1955, 1957) support the view that the Danish fishermen operate over a considerably wider field, covering the whole Baltic, than the Gothland and, in particular, the Blekinge fishermen. This is due to the fact that the Danish and German vessels are large and very seaworthy; they are equipped with powerful engines, and so are capable of making long voyages even in winter. In this respect the Blekinge and Gothland fishermen as well as the Polish are not so well off; they are often prevented from fishing for salmon during the cold season by rough and stormy weather or drift ice. Consequently, the bulk of the catch is taken in spring and autumn despite the fact that there are plenty of salmon to be had all over the area even in the depth of winter.

It was pointed out in the foregoing section that the Blekinge and Gothland fisheries sometimes exhibited widely different size-group distributions in one and the same season. In the former fishery, small salmon were predominant in early summer and, particularly, early autumn, whereas in the latter they were most plentiful in late autumn and winter. This is to be ascribed partly to the different methods of fishing employed, and partly to the effects of the migratory behaviour of the salmon, as outlined above. The smallest salmon, which obviously spend their first winter at sea in the vicinity of Gothland, quite naturally become the object of the intensive drift-line fishery which is carried on in these localities at that time of the year. Consequently, the proportion of salmon weighing less than 3 kg. and, in particular, of those weighing between 0·5 and 1 kg. must be comparatively high in winter. This feature will be especially marked if in a particular year the number of migrating smolts is exceptionally high and the survival ratio is also high. On the other hand, towards late spring, when fishing activities in Gothland are extended to the use of nets, it is but natural that the proportion of larger salmon increases as the small salmon are not so easily caught in the wide-meshed nets. This also accords with the curves in Figure 8. It may also be the case that small salmon are more sensitive to high temperatures than large. If so, small salmon would move into deep water earlier in the spring than large fish, and remain there until later in the autumn.

If we may judge from the results of the marking experiments, small salmon do not approach the Blekinge coast until towards the second summer. At that time they weigh from 1·2 to 3 kg. On the assumption that the age-group distribution follows the normal pattern, the stock of small salmon

may be expected to be larger than that of the salmon one or two years older which are present at the same time. This would suggest that the proportion of small salmon in the Blekinge fishery ought to be markedly high in August–September, and this actually appears to be the case, as may be seen in Figure 6. The very profitable spring fishery is mainly carried on with nets, and the catch of small salmon is therefore comparatively small.

The Bothnian Sea and the Gulf of Bothnia

In the foregoing, it has been shown that during their sojourn in the Baltic proper the salmon avoid the upper layers in summer, when the water temperature is high. Owing to the difficulties of fishing for salmon in considerable depths of water, the catch in summer is negligible. How, then, does this harmonize with the fact that the summer salmon fishery yields very good catches throughout the Gulf of Bothnia? It is true that the mean temperature of the surface water is no more than 7°–8° in June, but in mid-July it is about 14° in both the Bothnian Sea and the Gulf of Bothnia and even higher at the end of the month. In August the mean temperature increases to about 15°. There is no doubt that in certain localities in the skerries, where this summer fishery takes place, the temperature may even exceed 15°. Thus, the salmon caught there do not move into deeper water when the temperature of the surface layer rises. The explanation for this must undoubtedly be sought in the fact that two different stages in the salmon's life-cycle are involved.

The salmon caught in the Baltic are migrating in search of food while those caught in summer in the Gulf of Bothnia are, no doubt, migrating chiefly for spawning purposes. In the former state, as has already been pointed out, the salmon are markedly sensitive to high water temperatures whereas it may be the case that salmon migrating for spawning purposes are not so sensitive. In support of this supposition, it may be mentioned that in several rivers the salmon ascend at times when the water temperature is considerably above 11°–12°, namely, the critical temperature for salmon migrating in search of food. According to MELIN (1938) the mean temperature in the northern Swedish rivers is 15°–16° in July and August, and sometimes reaches 18°–19°. In the southern Swedish rivers the mean temperature is 17°–18°. It would thus seem likely that the salmon becomes less sensitive to temperature during its sea life, in association with the onset of sexual maturity and the spawning migration instinct. In such circumstances it is not surprising that the summer fishery in the Bothnian Sea and the Gulf of Bothnia takes place at considerably higher temperatures than the fishery in the Baltic.

In this connexion, it has been assumed that these salmon are on a spawning migration, and several facts indicate that this is so. Thus, in the region in question the salmon are caught close inshore among the skerries, chiefly with traps and other similar tackle. On the other hand, no salmon are encountered in the open sea at this time of year and none rise to the bait, which shows that they are not in search of food. Furthermore, according to information provided by the fish marketing associations, their sexual organs are usually well developed, which indicates that spawning is not far ahead. As shown in Figures 11 and 13, salmon weighing more than 8 kg. dominate the catches taken in the best summer season, namely, June and July. The average weight is therefore high and seems to be almost equal to that usually recorded for salmon caught in the rivers, namely, 8–9 kg.

Table 8

Monthly salmon catch in northern rivers, expressed as percentages of the annual catch

	Ljusne, Ljusnan				Forsmo*), Ångermanälven				Norrfors*), Ume älv			
	June	July	Aug.	Sept.	June	July	Aug.	Sept.	June	July	Aug.	Sept.
1951	6·2	58·4	28·9	6·5	0·2	55·0	43·3	1·5	3·7	76·6	18·9	0·8
1952	–	80·0	19·1	0·8	0·2	93·4	4·6	1·6	17·1	67·5	15·4	–
1953	22·9	39·5	31·7	5·9	11·9	44·1	40·8	–	21·2	64·3	13·4	1·1
1954	17·2	36·4	31·1	15·3	3·3	31·5	59·2	5·4	13·5	46·5	38·2	1·8
1955	–	70·2	20·1	9·7	4·2	78·6	15·5	1·7	3·4	85·9	10·7	–
Average	10·0	56·5	26·5	7·0	4·5	56·2	37·4	2·0	12·3	66·6	20·3	0·8

	Edefors*), Lule älv				Näsbyn, Kalix älv				Torne älv**)			
	June	July	Aug.	Sept.	June	July	Aug.	Sept.	June	July	Aug.	Sept.
1951	14·4	74·7	10·9	–	9·1	89·6	1·3	–			–	–
1952	41·8	55·4	2·8	–	23·3	76·7	–	–			–	–
1953	46·8	44·8	8·4	–	66·7	33·3		–	–	–	–	–
1954	28·1	52·3	19·5	–	1·5	98·5	–	–	–	–	–	–
1955	17·2	76·8	6·0	–	16·0	84·0	–	–	–	–	–	–
Average	32·4	58·1	9·5	–	30·5	69·3	0·2	–	25·0	74·0	1·0	–

*) A deduction of two weeks, cf. the text.

**) The figures, taken from NORDQVIST, relate to the period 1882–1902.

Since salmon on spawning migration constitute the bulk of the summer catch, it would be reasonable to expect a fair agreement between the catches from the sea and the rivers, respectively. To elucidate this question, data have been obtained from a number of the more important salmon rivers on the salmon catch for fortnightly periods. It should be mentioned that among the stretches of river to which the data relate, only those in the Ljusnan and Kalix älv are situated near the river mouth. Thus, the time of the catch in these areas corresponds fairly well to the beginning of the salmon run in these rivers. In the other rivers the fishing grounds are situated fairly well up the river; no doubt allowance must be made for the time taken by the salmon — possibly some weeks — to travel from the mouth of the river to the fishing grounds. To ascertain the time at which the run began in the lower reaches of the river, about two weeks should be deducted from the date of the catch. The figures in Table 8 have been so treated and the percentage catch in each month was computed with the amended figures. The table also incorporates the returns made by O. NORDQVIST for the Torneälv. The average catches for the years 1951–55 are illustrated graphically in Figure 17, which also shows the catch curves for the neighbouring sea areas.

The curves clearly suggest the existence of some mutual correlation and also show, as may quite naturally be expected, that the main catches were taken somewhat later in the rivers than in the sea. It is also evident that in the years under review the run usually took place later in the southern rivers than in the northern. Further, the time elapsing between the main catches in the neighbouring sea area and the run in the river is shorter in the case of these rivers than in those entering the Bothnian Sea. This seems to indicate that while they are in the sea the salmon remain longer off their native rivers in the Bothnian Sea than do the fish in the northern parts of the Gulf of Bothnia.

The assumption that a correlation exists between the summer catch in the sea and the catch in the neighbouring rivers is supported by the fact that in

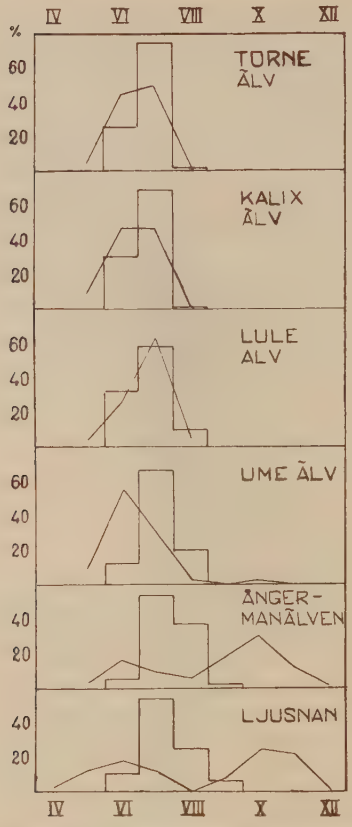

Figure 17. Comparison between the monthly catch in certain Swedish rivers (histograms) and the catch at sea off the mouth of the river, expressed as percentage of the annual catch (curves).

1953 a deviation from the usual pattern was experienced in all localities. In that year, as shown in Table 8, the June catch in all the rivers constituted a higher percentage of the annual catch than in other years; this year was particularly so for the Ljusnan, Ångermanälven, and Kalix älv. This means that in 1953 fishing in these rivers commenced earlier than usual. A correspondingly early start in the salmon fishery was also experienced that year on the grounds off the mouths of these rivers. Thus, it emerges from Figs. 10 and 12 and even more clearly from Table 9 that in these localities the catch taken during the first months of the actual fishing season in 1953 constituted a higher proportion of the total than the average for the entire period. It has already been pointed out by O. NORDQVIST (1906, 1924) that in some Finnish and Swedish rivers there is a certain correlation between the time of the salmon run and the height of the water-level. The existence of such a correlation between fish migrations and water-level has since been emphasized by several scientists. This accords with conditions prevailing in 1953, as information obtained from the Swedish State Institute of Meteorology and Hydrography states that in 1953 the spring flood was recorded earlier than usual in the Ljusnan, Ume älv, and Kalix älv. This is especially true of the Kalix, in which the spring flood was recorded as early as the beginning of May whereas it usually occurs at the beginning of June. In April, the Ångermanälven, for which records are usually kept, already contained far more water than usual. Hence, the early salmon run that year was due to an early spring flood in the rivers, which, no doubt, also affected the sea, even at some distance from the coasts. Owing to their marked homing instinct, it is but natural that the time at which salmon return to their native waters varies and depends upon the time at which the outflow from the rivers is greatest.

As proof of the fact that the salmon caught in summer in various parts of the sea are mainly fish on their way to their native rivers, reference may be made to the recapture of some small salmon, weighing only a few kg., which had been caught and marked on the coast of Norrbotten (ALM, 1941, 1943; CARLIN, 1953, 1957). Most of the recaptures were made within a year of marking in the rivers debouching into the sea nearby or in the neighbouring archipelago. Only a few of them were recaptured in other parts of the Baltic.

Table 9

Weight of salmon landed at the beginning of the season at ports in the Bothnian Sea and the Gulf of Bothnia
(expressed as percentages of the annual landings)

Port	Gävle		Härnösand		Umeå	
Month	IV	V	V	VI	V	VI
Average	3	13	3	16	9	56
1953	7	13	5	29	24	56

Port	Luleå		Kalix		Nikkala	
Month	V	VI	V	VI	V	VI
Average	2	27	8	45	4	45
1953	3	32	9	72	6	62

The results of the different marking experiments are not quite uniform, however. The more southerly the location of the position of marking, the more scattered are the recaptures. This is particularly true of some markings made off Umeå and at Holmöarna (STRANDBERG, 1957) while recaptures of salmon marked at the northernmost stations in the skerries off Torne and Haparanda are more noticeably concentrated in the neighbouring skerries and rivers.

As an instance of the correlation between the salmon caught in summer off the Norrland coast and those ascending the river to spawn, we may refer to some information published by OLOFSSON (1926, 1932). This author points out that the very rich stocks of small salmon weighing from less than 1 kg. up to 3 kg., which were encountered off the coasts of the Västerbotten and Norrbotten Counties in 1925 and 1931, coincided with extraordinarily good runs of salmon of the same size in both of these years.

In view of these facts, it seems justifiable to conclude that the salmon remain in the archipelago off the river mouths only for a very short time and are on route to their native rivers. Thus, the summer catch in the Bothnian Sea is composed chiefly of salmon just about to ascend the rivers flowing into that sea; they are most unlikely to contain salmon on their way to the grounds in the northern Gulf of Bothnia and the rivers debouching into it. The fishing in the latter regions is concentrated on salmon travelling more or less directly from the open sea to these localities. The results of the marking experiments mentioned above suggest that when passing through the Kvarken vicinity the salmon tend to approach the shore to some extent; this tendency becomes gradually more marked the further north they travel in the Gulf of Bothnia. It is not very probable, however, that the bulk of the salmon migrating towards the Gulf of Bothnia to spawn travel close inshore. If it were so, the salmon fishery carried on near the northern coasts of the Bothnian Sea and the southern coasts of the Gulf of Bothnia should rest partly on the salmon seeking the rivers flowing into these waters, partly on those making their way to the northern rivers. In such circumstances the landings in, for instance, the Västernorrland and Västerbotten Counties would exceed those of Norrbotten County by considerably more than is actually the case.

The assumption that the salmon do not in general approach the coasts at an earlier stage of their migration is also supported to some extent by the results of the smolt-marking experiments carried out in the Lule älv (CARLIN and JOHANSSON, 1957). Among the fish tagged, only one fairly large salmon

was recaptured in the Bothnian Sea, even in autumn, while a great many of them were captured in summer in the northern part of the Gulf of Bothnia. This indicates that they entered these waters directly without having previously travelled close inshore.

Finally, reference may be made to the close correspondence between the annual catches taken in the coastal fisheries off Piteå, Luleå, and Kalix-Nikkala (Fig. 12). The main catch is taken somewhat earlier in the Umeå fishery, which may perhaps be attributed to the fact that the catch in this area comprises quite a number of salmon which are migrating northwards and appear in these waters some time before approaching the northern coasts of the Gulf of Bothnia.

It is impossible to state with certainty the dates on which the salmon appearing in spring and summer in various regions of the Bothnian Sea and the Gulf of Bothnia left the Baltic. It is possible that the migration from the Baltic takes place throughout most of the year, but it undoubtedly occurs principally in autumn and winter. The heavy concentration of catches in the autumn in Kalmar, Östergötland, Södermanland, and Stockholm Counties and the tendency for the main catch to be taken in late autumn and winter in the last-named counties seem to suggest that the salmon caught in these localities are on their way northwards. The fact that in the course of the fishing season the size of the salmon gradually decreases would seem also to indicate that in this stage of the migration the large salmon leave the Baltic earlier than the smaller fish. In late winter and early spring these salmon most probably favour the open sea, where ice obstructs fishing. As mentioned above, they do not approach the coasts and become the object of the above-mentioned fishery until very late in the spring.

In discussing the salmon on spawning migration in the Gulf of Bothnia the salmon caught in the Gulf of Riga must also be taken into consideration. As was mentioned above, these salmon were also caught in summer, and we may assume that they were collecting there before ascending the river Düna and other Latvian rivers for spawning.

It was mentioned above that a valuable salmon fishery is carried on in autumn in the Bothnian Sea. There is no parallel fishery in the Gulf of Bothnia, at any rate in its northern parts. At Kvarken, which forms part of the area covered by the Umeå association, the catch, as previously pointed out, rises slightly in late autumn. In the light of the information given above, namely, that the salmon caught in summer in the Bothnian Sea and the Gulf of Bothnia are on their way to the spawning grounds, it is justifiable to conclude that the salmon caught in autumn in the Bothnian Sea are migrating in search of food. That they do not belong to the former group is proved by the simple fact that the majority of the salmon of that group have already completed their ascent of the rivers a long time before the autumn salmon appear in abundance. As pointed out earlier in this paper (p. 412), the size-group of 3–6 kg. invariably predominates in the autumn catch (cf. Fig. 11). The average weight of the salmon caught is, therefore, considerably lower in autumn than in summer. This, too, goes to prove that two different groups are involved. It is possible that small salmon weighing less than 3 kg. are also included in these catches, though they may be entered as sea trout in the statistical records. That the autumn salmon do not belong to the same group as the salmon caught in summer is also indicated by the fact that, according to information provided

by the fish marketing associations, their sexual organs are rarely well developed. Clear evidence of the fact that the autumn salmon are migrating in search of food is furnished by the means by which they are caught, namely, almost exclusively hook and line; furthermore they are often caught at some distance from the coast.

It is impossible to say exactly when the salmon caught in autumn enter the Bothnian Sea. They may have appeared in these waters almost simultaneously with the first catches but, on the other hand, they may well have been present before that time. As stated above, the catches usually reach their peak in October, though not until November in some years, as, for instance, 1954 and 1955. If a large number of salmon had migrated northwards in late summer the natural consequence would have been richer catches in September and, certainly, October. It seems justifiable to assume that, like the salmon in the Baltic, the salmon migrating in search of food avoid water layers of a temperature above 11°–12°. This means that if they had entered the Bothnian Sea in late summer, they presumably remained at first in deep water, where they are difficult to catch. In that case, they would have returned to the upper water layers in September when the temperature begins to decrease; the mean temperature at the lightships in the Bothnian Sea at this time is 12°–13°. This return to the upper layers would have been even more marked in October when the mean temperature at the lightships ranges from 7·7° to 8·7°. As, however, they were not caught in any large quantity during that period, it must be assumed that, at any rate in 1954 and 1955, these salmon did not migrate to the Bothnian Sea until the end of the year. In other years in which the main catch was taken in October, migration may have taken place only a short time before, though certainly earlier than in 1954 and 1955.

The possibility cannot be excluded that the salmon had already entered the Bothnian Sea early in summer but had stayed in deep water. On the other hand, it is not very probable that they were present in large numbers in the Bothnian Sea earlier in the year. If so, they ought to have appeared in the upper water layers, where they could be reached by fishermen, in spring and early summer before the temperature had become too high. The smaller size of the salmon caught at the very beginning of the fishing season (cf. Fig. 11) seems to suggest, however, that at that time of the year the catches did include salmon belonging to the group now under discussion.

In this connexion it may be recalled that several scientists (Alm, 1924; Jacobsen and Johansen, 1921; Svärdson, 1956) have established a correlation between sea water temperature and the data of the run of salmon of a particular age-group. Though the salmon caught in autumn in the Bothnian Sea have been considered, for purposes of discussion, as salmon migrating in search of food, there is no reason to believe that the same group may not migrate in the following year for spawning purposes. On the contrary, this would seem most likely. The urge to spawn and the beginning of sexual maturity, which, apart from the age factor, are initiated by a high water temperature may also have a bearing on the date of migration in the Bothnian Sea.

It goes without saying that it is difficult to draw a hard and fast line between the salmon discussed above, which are migrating in search of food, and those mentioned earlier, which are presumably migrating from the Baltic to the spawning grounds later in the autumn and winter. While the former become the object of profitable fishery in the Bothnian Sea in autumn, the latter owing

to the difficulties of fishing in winter, do not form part of the catches until the following spring and summer when they are on their way to the spawning grounds.

A group of salmon not to be forgotten is that consisting of fish which have entered the rivers to spawn and returned again to the sea in search of food. Marking experiments with such salmon (cf. p. 420) show that they are caught in large numbers, particularly in the Baltic but also in the Bothnian Sea and the Gulf of Bothnia. Some are caught in spring, obviously shortly after having spawned and left their native river. But they are even commoner in autumn when they evidently form part of the stock of salmon, migrating in search of food, encountered in the Bothnian Sea. Recaptures of previous spawners in the actual summer months are, however, rare.

A factor which ought also to be taken into account when migrations are under review is the fluctuations in the supply of appropriate salmon food in different parts of the Baltic.

Irrespective of the date on which the salmon caught in autumn in the Bothnian Sea migrate to that area and of the reasons for their migration, it is obvious that they occur in these waters in fairly large numbers. The quantity of these salmon caught, calculated by weight, is sometimes larger than the summer catch of salmon on migration to the spawning grounds. Because of their considerably smaller size the first mentioned group is by far the most numerous. It is surprising that these salmon do not travel farther north and enter the Gulf of Bothnia. The fact that there is no autumn fishery in the gulf suggests, however, that there are no large stocks of salmon there in search of food. Attempts have been made by both Swedish and Finnish fishermen to employ the same methods of fishing as those used in the Bothnian Sea, but with very little success. Hence it would seem justified to draw the general conclusion that, as a rule, only salmon migrating to the spawning grounds are encountered in the Gulf of Bothnia. In a few instances it was evident, however, that salmon in search of food were also present, the result being fairly rich catches in the southern parts of the Gulf of Bothnia. Reference may also be made to the above-mentioned autumn fishery in the Umeå area, though the catches are fairly small.

Finally, it has been proved through certain marking experiments that salmon in search of food are sometimes caught in this area (ALM, 1938, 1941, 1943); thus, two small salmon, which had been marked in the Weichsel as smolts in the preceding year, were recaptured in 1939 in the Gulf of Bothnia. As regards the salmon's homing instinct, it must be accepted as a fact that these small salmon only made occasional journeys to northern waters. Further, two smolts which had been tagged in the Kumo River were captured in the Gulf of Bothnia. And, lastly, from these small salmon which had been tagged off the coast of Norrbotten, two were recaptured in other parts of the Baltic. One of them was captured off the mouth of the Kumo River a year after marking, and had attained a length of 86 cm. and a weight of 7·6 kg. The other was captured one year later off Vindau in Latvia; it measured 97 cm. and weighed 11·6 kg. It may well be imagined that a part of the heavy catches of small salmon taken in 1925 and 1931 consisted of salmon migrating in search of food or of salmon which had not migrated to the Baltic but had stayed in the Gulf of Bothnia after leaving their native rivers. The presence of abundant stocks of small salmon weighing less than 3 kg. which, as stated on pp. 408 and 415 were encountered in 1954 not only in the Baltic but also in the Gulf of Bothnia

suggests that part of the salmon stayed on the northern grounds after leaving the spawning grounds.

Such behaviour must be considered exceptional, however. That quite young salmon migrating from the most northerly rivers flowing into the Gulf of Bothnia usually seek the southern parts of the Baltic is certainly borne out by several marking experiments (Henking, 1913, 1916; Alm, 1934; Carlin, 1957) and in particular by the high smolt age of the small salmon formerly caught in large quantities off Poland in autumn (Dixon, 1931). A correspondingly high smolt age is recorded only for the northernmost spawning rivers.

To establish the truth of the foregoing hypothesis respecting the migrations of the larger salmon in the Baltic and in the northern regions, in particular, extensive marking experiments are necessary. This applies especially to the salmon caught in autumn in the northern part of the Baltic and in the Bothnian Sea, and also to those taken in the latter area in summer. It would be of special interest if the date could be ascertained at which the salmon caught in autumn in the Bothnian Sea commenced their spawning run and whether this is performed both in the rivers flowing into the Bothnian Sea and in those debouching in the Gulf of Bothnia.

Further, investigations are needed into the food the salmon rely on and on their food requirements at different times. Studies are also needed on the state of development of the sexual organs of salmon caught at different seasons by means of different tackle. The result of such investigations might contribute to our knowledge of salmon migration.

V. Summary

The catch of salmon in various parts of the Baltic is more or less concentrated on certain seasons. The pattern is repeated every year and is connected primarily with spawning and feeding migrations. It also depends to some extent on the weather, and the fishing vessels and the gear employed.

In the southern Baltic the main catch is taken in winter and little fishing, if any, takes place from June to October. In the central Baltic the heaviest catches are taken in spring and autumn. Winter fishing is less profitable, chiefly owing to the technical difficulties encountered during that season by the fishermen, and in July and August the catches are insignificant. In the northern Baltic fishing is confined to late autumn.

In the Bothnian Sea the richest salmon catches are taken sometimes in summer (June and July), sometimes in autumn (October and November, in particular). In the northern Gulf of Bothnia fishing is most remunerative in summer (June and July). The autumn fishery is only very small.

The fishery in the Baltic which goes on throughout most of the year and the autumn fishery in the Bothnian Sea both depend mainly on salmon migrating in search of food. These fish are sensitive to water temperatures higher than 11°–12°C. When the temperature exceeds this value they seek deeper water, presumably between 15 and 20 m., the level at which the thermocline occurs. When the water temperature decreases in late summer the salmon again return to the upper water layers.

A temperature of 11°–12°, the critical value for salmon, is reached at the beginning of June in the southern Baltic, but not until the end of that month

or the beginning of July in the central and northern Baltic and the Gulf of Bothnia. At some time in late summer or autumn the falling temperature reaches the critical value in the latter half of September in the north, but in the southern Baltic this value does not occur until October.

For various reasons it is difficult to fish for salmon in a considerable depth of water, irrespective of whether nets, fixed lines, or drift-lines are used. Fishing is therefore confined more or less to the upper layers and is, of course, limited to the season at which the salmon appear in those layers.

The salmon's sensitivity to temperature during feeding migrations and the restriction of fishing to the upper water layers account for the suspension of salmon fishing in the Baltic in the hottest months of the year and the longer period during which fishing is suspended in the southern Baltic. Likewise, the date on which the autumn fishery begins in the Bothnian Sea may reflect the temperature conditions at that time of year.

Salmon travelling about the Baltic in search of food are encountered throughout the year. It is uncertain whether the fish caught in autumn in the Bothnian Sea entered that region in the previous summer to spend their first period in deep water or whether they remained in the Baltic until late summer or autumn before migrating.

The salmon caught in summer in the Bothnian Sea and the Gulf of Bothnia are chiefly fish on their way to the spawning grounds. They are caught principally at the time of year at which they enter the rivers, i. e., in summer. In that locality the mean water temperature at sea is 7°–8° in June, about 14° in July, and well over 15° in August. In the rivers the mean temperature rises to 16°–17°. Hence, these salmon are less sensitive to high water temperatures than those migrating in search of food. Most probably they spend the latter part of the winter and spring in the open sea and do not approach the shores bordering the rivers in which they spawn until a short time before the run.

To throw more light on salmon migrations in the Baltic area, it is necessary to carry out extensive marking experiments with large salmon and to investigate the salmon's feeding habits and the development of their sexual organs.

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Notes on Recent Atlantic Salmon Investigations in the USSR

By

G. Nikolsky

In 1956 the total catch of Atlantic salmon in the USSR northern waters was 10,000 cwt. During the period from 1946 to 1956 the total yearly catch of salmon in this area ranged from 8 to 18 thousand cwts. (Baltic Republics excluded). In 1956 the catch of salmon was 7,000 cwts. in the Arkhangelsk region and 4,900 cwts. were taken from the Petchora. During recent years the total catch of salmon amounted to 10,000–20,000 cwts. Liberations from hatcheries in 1956 amounted to 37·4 million salmon fry and 1·1 million fingerlings.

Investigations by the Institute of Freshwater Fisheries

(Contributed by Prof. V. Ivlev)

These have shown that the spawning grounds of the northern form of Atlantic salmon studied by V. S. Mikhin fall into two categories in accordance with their hydrological regime, namely:—

(a) spring water spawning grounds with a water temperature in winter of 1° to 3°C. and a short period of ice cover (Jemtsa River — tributary of Northern Dvina);

(b) springless spawning grounds with the water temperature in winter about 0°C. and a durable ice cover (Kem, Varzuga, and some other rivers).

On the spawning grounds of the first type eggs develop more rapidly than on spawning grounds of the second type. Fry are hatched a month earlier and therefore the feeding period of the young is longer and their growth better.

The number of eggs in a redd seldom exceeds 1,000, usually much less, which points to a great loss of eggs in the process of spawning, even on the assumption that a salmon makes not less than three redds. The greatest losses of eggs occur at the time when the eggs are deposited by a female salmon and buried in a redd, for considerable numbers are carried away by the currents. Thus the efficiency of natural spawning is very low and depends on a number of conditions, the most important being:—

(a) fluctuations of water levels and the freezing of the spawning grounds;

(b) type of bottom and velocity of currents;
(c) pollution; and
(d) damage to redds near river banks caused by ice.

The sex ratio of the young salmon varies both for the same year in different rivers (Varzuga, Kola, and Jemtsa) and for the same river in different years. Smolts of the Varzuga River descend mainly at the age of 3 years but older age-groups occur among the Kola smolts. Backcalculations show that there is but a little difference between the growth-rates of the young in these three rivers. Age for age, however, the average weight of the Kola smolts is higher than that of the Varzuga smolts. By comparing the Kola and Jemtsa parr of the same age it was found that the Jemtsa fish were somewhat heavier than those of the Kola.

The Varzuga fishery is based on "autumn" salmon, "summer" salmon (mezhen) being second in importance. The smallest individuals belong to the "summer" group, whereas, on the average, the largest ones are those belonging to the "spring" group (zakroika). However "spring" salmon never reach the maximum size of "autumn" salmon. By the close of the spawning run "summer" salmon become larger in size whereas "autumn" salmon become smaller. The main part of the Varzuga salmon consists of fish which have spent just over one year in the sea (1+ group of sea life). The growth-rate of the different forms of Varzuga salmon is almost the same. It varies from year to year depending on hydrological changes. The growth-rate of the Varzuga males in the sea is somewhat higher than that of the females.

Groups of salmon differ among themselves in the duration of their marine period and their river period. Different groups of the Varzuga salmon mix on the spawning grounds. The sex ratio between males and females on the spawning grounds is about 1 to 2.

According to M. N. Melnikova the number of the Varzuga salmon participating in spawning is 10% to 20% (with some yearly deviations) of the total stock entering the river. A rough estimate shows that the commercial return of Atlantic salmon (from eggs) ranges from 0·11 to 0·34%.

In 1955 G. G. Galkin made a study of the survival of young salmon under river conditions by liberating three size groups in the Peterupe River, flowing into the Gulf of Riga. The three groups were as follows: Group III, 150,000 fry; Group II, 5,300 parr (average weight — 1·7 g.); and Group I, 1,000 parr (4·0 g.). An automatic trap which recorded all descending fishes and prevented the ascent of spawners to spawning grounds was permanently set up in the estuary of the river. Since all the young fish had been tagged it was possible to estimate survival rates for each size group. The aim of this work was to obtain an estimate of the survival rate of the young fish raised at hatcheries. As the productivity of any hatchery is limited mainly by the capacity for rearing and depends only to a small extent on the supply of ova, it is very important to know the absolute values of the survival rates of the young during their river life. The starting points are:— (a) Equal survival rates of salmon during their sea period (from smolt to sexual maturity) and (b) the effort required to rear young fish of different sizes. Estimates show that at hatcheries approximately the same effort is required to raise one smolt (two-year-old) weighing 20 g. or 25 parr (fingerlings) weighing 4 g. each, or 100 1·5 g. parr or 200 to 300 fry.

Relative survival rates were higher for larger young fish but the efficiency

of a hatchery as a whole depends on the number of fry reared and their survival rate (which is related to size).

The catches of 1956 contained:—

Group I — 0·08% (average weight 26·4 g.)
Group II — 1·23% (– – 24·6 g.)
Group III — 0·4 %(– – 16·3 g.)

All the fish of Group III have not yet descended and some may descend in 1957.

Work on technical problems connected with the rearing of young salmon has been developed along the following two lines, namely, (a) investigations of the comparative value of various kinds of artificial food in raising fry in tanks and (b) increasing the productivity of fish ponds in distant northern areas. N. I. JANDOVSKAYA, who worked on the first problem came to the following conclusions. The best effect was achieved by using minced beef spleen to which some vitamins (A_1, B_1, B_2, D, B_{12}, and others) as well as up to 20% carbohydrates were added. Thus the efficiency of rearing (i. e., increase in growth-rate and reduction of mortality rate) became 45% higher. An attempt to use dry blood as a main food yielded unsatisfactory results. The above conclusions are based on piscicultural indices (growth and mortality) as well as on histo-physiological analysis of liver done by K. A. FAKTOROVITCH.

The best food for young salmon at the earliest stages of development was shown to be live food (*Enchytraeus albidus*). Work on mass cultivation of *Enchytraeus albidus*, which had been begun earlier, was continued in 1956 by I. V. IVLEVA. The annual production of *Enchytraeus albidus* at many hatcheries now amounts to hundreds of kilogrammes.

The results of the work carried out by N. S. JALYNSKAYA showed that at high latitudes the feeding capacity of ponds situated on peaty soils may be increased with the help of mixed mineral fertilizers (phosphorus+nitrogen+potassium). The fish productivity of such ponds in the vicinity of the Kola Bay (69° N.) was thus increased to 60·6 kg. per hectar.

Investigations by the Polar Institute of Marine Fisheries and Oceanography

(Contributed by I. LAGUNOV and V. ASBELEV)

It has been shown that the age (and to a certain extent sex) composition and fecundity were different for stocks of Atlantic salmon entering different rivers, i. e., the Kola, Tuloma, and Kolvitsa. On an average one hundred spawners produced 811,000 ova for the Kola stock, 421,000 ova for the Tuloma stock, and 517,000 ova for the Kolvitsa stock.

In the Kola stock 4·2 to 13·9% of the brood survived for a second spawning migration and 0·09 to 0·4% for a third. For the Tuloma and Kolvitsa stocks 0·3 to 2·6% survived for the second spawning migration. Survival for the third migration has not been observed.

At present reproduction in the Kola stock is taking place under somewhat unfavourable conditions. While the adjacent stock (i. e., the Tuloma stock) has been increasing, the stocks belonging to the rivers entering Kola Bay have been stationary, the average catch being 26% of migrating fish.

The Kolvitsa stock could doubtlessly permit of more than a 50% catch,

Table 1

Average percentages of the various age-groups of salmon migrating to different rivers

River	Age-groups (%)							Second migration	Number of fish
	3+	4+	5+	6+	7+	8+	9+		
Tuloma	8·6	35·3	38·2	14·5	2·2	–	–	1·2	4390
Kola	5·3	22·7	30·4	27·4	7·1	0·8	0·2	6·1	1600
Kolvitsa	30·6	39·0	21·8	7·0	0·75	0·05	–	0·8	1780
Petchora	0·06	4·6	67·7	20·19	2·5	0·23	0·02	4·7	37,950

since, with the average catch amounting to 46% of the population, the stock is still increasing. Here the earlier maturity of the Kolvitsa migrants may be a contributory factor.

At present we know the fluctuations of two generations of Atlantic salmon originating from a known number of spawners of the Tuloma and Kolvitsa stocks. The return coefficients are 1:3·8 and 1:7·5. Knowing the age compositions of these generations we can state that the present increase in the abundance of the stocks under consideration is a result of changes in the return ranging from 1:3·2 to 1:7·7. The percentage of total survival for Atlantic salmon is by no means high. A rough estimate shows that at present it does not exceed 0·1%. For the Kolvitsa brood alone it is 0·06%. The general trend of the return of migrants belonging to the Kolvitsa brood of 1950 points to the fact that in this case an insufficient number of migratory males did not affect the numerical strength of the brood.

In 1950 and 1951 poor catches of salmon in Kolvitsa Bay, Kola Bay, and the Teriberk River, as well as the 1951 poor catches in the Petchora, resulted from the low yield of the brood from the 1945 spawning. It will be noted that this brood was also the poorest in the case of cod and haddock and very poor in the case of the Murman herring.

Some data on the age composition and abundance of salmon broods in the USSR are given in Table 1.

As may be seen from Table 1 salmon enter the Tuloma and the Kola mainly at the age of 4 to 6 years and the Kolvitsa at the age of 3 to 5, while 5- and 6-year-olds nearly always prevail in the Petchora. Thus the Kolvitsa salmon are characterized by a shorter span of life and a relatively earlier maturity.

The salmon stock spawning in the Kolvitsa has increased during recent years, the average catch of migratory fish being 46%, whereas that of the stocks spawning in rivers entering Kola Bay has been stationary, the average catch of migratory fish being only 26%. This difference between the permissible catches is not dependent on differences in the natural conditions in the river and in the sea, but on the survival of spawners (see Table 2).

These coefficients by no means point to a high total survival rate of salmon, since the average fecundity of a Tuloma female is 10,400 ova and that of the Kolvitsa female is 8,500 ova.

At present instead of estimating the results of natural reproduction by the return from a known number of spawners we are beginning to estimate natural reproduction by the return from a known number of ova spawned, i. e., by the percentage of total survival. We have not yet found a way of obtaining an accurate estimate of the amount of ova spawned but this method of assessing

Table 2

The Tuloma salmon stock				The Kolvitsa salmon stock			
Year of spawning	Number of spawners, males and females	Abundance of brood	Return coefficient	Year of spawning	Number of spawners, males and females	Abundance of brood	Return coefficient
1945	2100	3508	1:1·67	1945....	135	535	1:3·96
1946	730	4997	1:6·84	1946....	165	425	1:2·57
1947	1540	5633	1:3·65	—	–	–	–
1948	810	5660	1:7·00	—	–	–	–
1949	810	6381[1])	1:7·85	1949....	220	834[1])	1:3·80
1950	1920	5582[2])	1:2·90	1950....	260	1289[2])	1:4·90

[1]) without 7+

[2]) without 6+ and 7+

Table 3

	Salmon stocks		
	Tuloma	Kola	Kolvitsa
Range of fluctuations in sex percentage.....	males 80–50 females 50–20	males 54–24 females 76–46	males 50–20 females 80–50
Range of fluctuations in average fecundity.....	10,600–9,950	13,900–10,500	10,400–7,100
Range of fluctuations in the number of ova for each hundred of spawners (males and females).....	485,000–207,000	1,000,000–533,000	834,000–411,000

the efficiency of reproduction seems to be more satisfactory, for observations showed that the sex ratio and the average fecundity vary from year to year. This results in the same number of spawners producing different numbers of ova in different years. This is illustrated by data in Table 3.

Table 3 shows that fluctuations in the reproductive value of migrating stocks are so significant that they cannot but affect the abundance of future generations.

Investigations carried out in the Petchora State Preserve

(Contributed by M. N. VLADIMIRSKAYA)

As in the past years studies were conducted at the places of spawning of salmon in the upper part of the Petchora River about 1650–1750 km. from its mouth. Only large specimens of salmon reach the upper part of the river. The spawning stock consists of 87% of first time spawners, 11% of fish spawning for the second time, and 2% of fish spawning for the third time.

Migrating male spawners compose 37% of all fish of the Upper Petchora. Dwarf males play an important part in spawning. Incubation lasts for about 250 days. In 1956, as in previous years, 90% of the young were composed of fish at the age 1+ and 2+ years. Older age-groups of 3+, 4+, and 5+ years old were but feebly represented among the young fish in the river.

The average length and weight compositions of the young in June are as follows:—

	1+	2+	3+	4+	5+
Length in mm.....	60	97	121	150	193
Weight in g.....	2·3	10·8	27·8	35·4	105·0

As a rule dwarf males in the Petchora River reach maturity at the age 2+ years; only insignificant numbers of the largest specimens mature at the age 1+.

The smolt descent usually takes place at the age 3+ years when they reach the length of 130 mm. and 250 g. in weight.

Small-scale tagging of the young salmon has been practiced since 1953 with the aim of assessing their distribution and migrations during their life in the river. Thus 550 specimens were tagged in 1953, 1000 in 1954, 527 in 1955, and 152 specimens in 1956. The fact was established that during summertime the young acquire a settled way of living; though in spring and autumn they are migrating along the river. The pike is the main predator of young salmon in the Upper Petchora, viz., young salmon were found in 5·1% of pike stomachs.

A certain skin disease of young salmon, apparently virus ephiloma (tentatively diagnosed by O. N. Bauer) is annually observed in the upper Petchora. No mortality of fish have been observed there as a result of the disease.

Acclimatization of Pacific salmon in the Barents Sea

Eggs of pink salmon, numbering 4,037,000, were transported by air from the Sokolovsky hatchery in the Sakhalin Island to the Taibolsky hatchery on the Kola River in October 1956. Wastage amounting to 5% occurred during the transportation. Incubation took place at the Taibolsky hatchery. About 3 to 5 millions of the young fish that reached the smolt stage were released into the Kola River in 1957.

This is a brief outline of the main reasearch work carried out on the Atlantic salmon in the USSR in 1956. We have not touched here upon the purely freshwater representatives of the salmon family. Nor have we dealt with the studies of salmon in the southern basins of the USSR.

All salmon investigations, as well as the other ichthyological investigations in the USSR are conducted in accordance with a general plan which is coordinated by the Ichthyological Commission of the USSR Academy of Sciences. The investigations started in 1956 will be continued in subsequent years.

A Device for Rapid Single-Handed Measurement of Shellfish

By

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Introduction

When recording the size measurements of shellfish, several methods are used, each of which has some disadvantages, especially when working in the field. With ruler, calipers, or measuring boards of various types, both hands are needed to operate the measuring device and hold the specimen being measured. Inevitably water, and often mud, is transferred to both hands from the sample under examination, and either time is lost while one hand is cleaned before measurements are written down, or two people are employed, one to measure, another to record. This is unsatisfactory, particularly if a large number of specimens have to be measured, or frequent samples are taken.

A measuring board has therefore been developed, which can be operated in any plane, with either hand, so leaving the operator's other hand free and dry to record for himself. It is accurate within 1 mm., and measures up to, and if necessary, past 100 mm. In use its speed compares favourably with alternative methods of measurement, and in construction it is robust for field work.

Description

The case and all moving parts are made from bakelite and brass to prevent corrosion; the instrument (Figs. 1 and 2) measures 10 in. $\times$ 6 in. $\times$ 3 in. and weighs 5 lb. A carrying handle is fitted.

Measurements are taken between a fixed zero plate (Fig. 1, 12) and a sliding parallel measuring plate (Fig. 1, 13) returned to zero after each operation by a coil spring (Fig. 1, 5) in tension. The specimen to be measured is picked up in one hand and the knuckles of that hand are used to press down the measuring plate while the specimen is inserted and orientated for the measurement required. When its size has been noted, the specimen is removed and the return

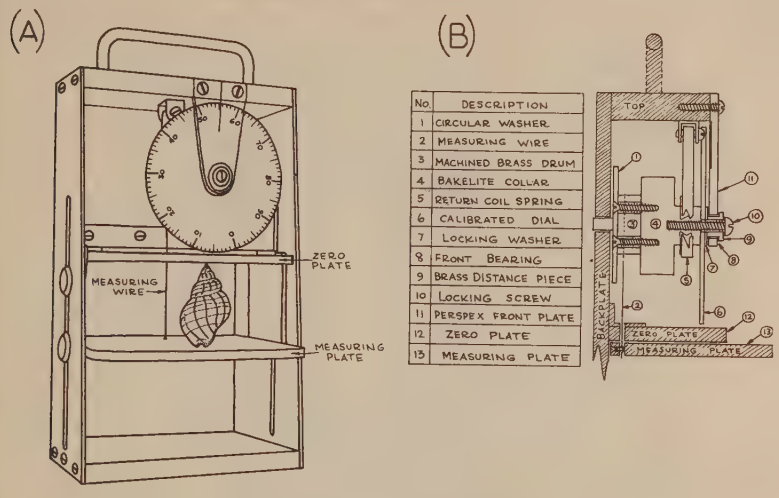

Figure 1. (A) Isometric view of device with *Buccinum*, length 55 mm., in measuring position.

(B) Diagram of spindle assembly with working parts numbered.

spring brings the measuring plate back to the zero position, in readiness for the next measurement. Results are read from a 4 in. diameter white plastic dial (Fig. 1, 6) connected by stainless wire (Fig. 1, 2) to the measuring plate, and engraved in black, at its rim, from 1–100, representing linear measurement between the plates in mm. The calibration of the dial rim in this way separates each mm. mark by 3 mm., ensuring easy reading of results, and reduction in errors during extended use.

The zero plate is screwed to the back of the case, allowing clearance at either side for the movement of the measuring plate guides. The wire linking the measuring plate and a machined brass drum (Fig. 1, 3) on the dial spindle passes through this zero plate at centre back, to give maximum space for measurement of large specimens. In construction, the circumference of this drum corresponds to a measurement of 100 mm. between the plates, but its diameter is critical, and machining must take into account the radius of the connecting wire being used. The dial spindle also carries the coiled return spring, confined on one side by a bakelite collar (Fig. 1, 4) and on the other by the back of the dial.

To ensure smooth parallel movement of the measuring plate, vertical slots are machined in the brass sides of the case, in which the screws holding the measuring plate guides move. These guides are held 1/16 in. from the case by spring washers to facilitate simple cleaning. The usual method of cleaning is to work the action of the instrument underwater until it becomes smooth.

In the event of the dial becoming out of alignment, allowance has been made for adjustment, by loosening the screw in the dial centre (Fig. 1, 10) and releasing the locking washer (Fig. 1, 7) which clamps the dial to its spindle. The dial is now free to move, and can be returned to zero and the locking washer re-tightened.

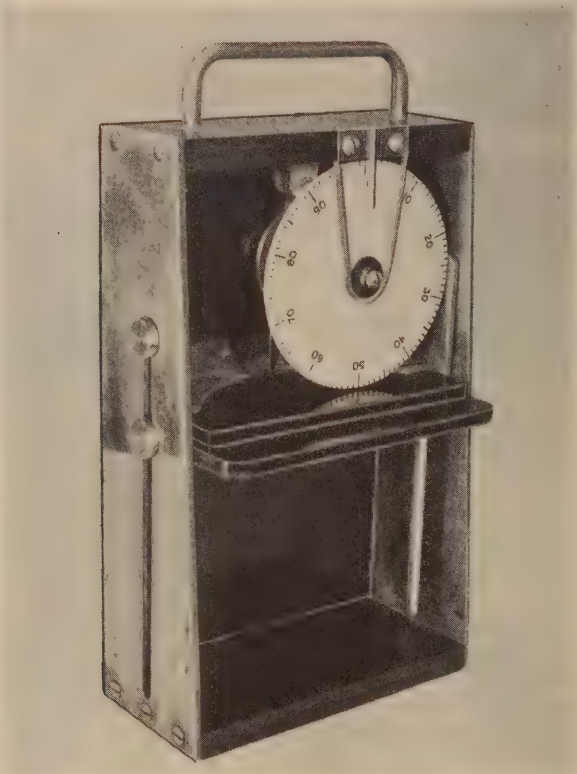

Figure 2. Photograph of the device for single-handed measurement of shellfish.

If it is required to measure specimens larger than 100 mm., the maximum distance between the plates can be increased during construction, and an additional part turn of wire taken on the brass drum. By this means a specimen larger than 100 mm. gives readings of one revolution of the dial plus a measurement of mm. on the second revolution, but, if this is done, care must be taken to prevent the two turns of wire on part of the drum becoming superimposed.

Small specimens — below 10 mm. — are difficult to insert precisely between the plates, but it is possible to insert a 10 mm. cube, plus the specimen, when measuring small individuals and to subtract this 10 mm. when recording. This method also improves the accuracy of the instrument at its lower limits.

The instrument has been used for measuring work in the field, and it is found that a rate of 1,000 individuals measured in 80 minutes can be comfortably maintained. This compares favourably with other methods, particularly when dealing with large samples.

L'Action des Grands Froids sur les Huîtres

Par

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Introduction

Les conditions atmosphériques exceptionnelles des trois dernières semaines de février 1956, firent de ce mois l'un des plus rudes que l'on n'ait veçu depuis de nombreuses années en France. Le thermomètre a fait une chute vertigineuse au-dessous de 0°C. enregistrant dans certains endroits la plus basse température (—23°C.) depuis 1893, le vent soufflant en tempête a atteint la vitesse de 180 km. à l'heure.

A la suite de l'intense chute de neige et en particulier des deux chutes abondantes des 14 et 17 février 1956, la couche de neige a atteint une épaisseur considérable (30–150 cm.) et a recouvert les endroits du sud-ouest de la France encore verglacés; une grande superficie de la mer était gelée près des côtes et les huîtres des parcs aussi. Toutes les claires étaient prises par les glaces et couvertes d'une couche superficielle de 5–10 cm. d'épaisseur.

En conséquence, on a annoncé des énormes dégâts (80%) dans les parcs à huîtres et les bouchots à moules causés par le froid, le gel, et la tempête.

Il m'a donc paru que des études sont nécessaires pour examiner la vraie cause provoquant la mortalité chez les huîtres exposées aux grands froids pendant l'hiver et qui est jusqu'ici obscure.

D'après la littérature, nos connaissances de l'action des grands froids sont fort réduites et les causes de mortalité peuvent être envisagées sous différents angles (Dollfus, 1922; Ranson, 1943).

Un petit nombre d'auteurs qui s'y sont intéressés ont signalé l'intervention des muscles adducteurs dans ce fait, sans expliquer le rôle qu'ils sont appelés à jouer (Spärck, 1927; Korringa, 1952). D'autre part, les recherches sur les muscles adducteurs des Lamellibranches sont fragmentaires.

Les recherches exposées ici comprennent d'une part les quelques résultats que j'ai obtenus dans les parcs à huîtres congelées, ainsi que les observations expérimentales faites aux laboratoires. D'autre part, une revue de la structure des muscles adducteurs chez les huîtres. Dans une troisième partie une étude sur l'action des facteurs telles que la congélation et la tempête sur la structure

Tableau 1

Lieu de déplacement	Mortalité %	Autres observations
1) Ronce-les-Bains: Pour examiner les huîtres dans les parcs d'élevage.	20	Pourcentage un peu plus élevé dans les parcs hauts.
2) Côte N.E. de l'Ile d'Oléron: Pour examiner les parcs d'huîtres et collecteurs.	10–40	Causé non seulement par le gel, mais aussi par l'envasement et l'ensablement à cause de la tempête.
3) Les deux rives de la Seudre: Pour examiner les collecteurs du naissain.	23 sur les coquilles, 30–40 sur les plaques d'ardoise	Les coquilles des chapelets collecteurs ont, en partie, éclatées sous l'action du gel prolongé, le pourcentage plus élevé sur les plaques d'ardoise suspendues à cause des frottements pendant la tempête. Rarement étaient les berceaux collecteurs détruits ou enfouis dans la vase.
4) Les côtes des Marennes (Bourcefranc et le Chapus): Pour examiner les huîtres des claires.	0	Température = 0°C. dans la couche voisine de la glace, mais à 10 cm. de profondeur elle était +5°C.

et la physiologie de ces muscles en expliquant la cause exacte de mortalité dont les conditions ne sont pas connues non plus.

Les résultats sont non seulement intéressants au point de vue purement scientifique, mais également au point de vue pratique et économique.

Les recherches ont été faites d'une part à la Station Biologique d'Arcachon (Université de Bordeaux) et d'autre part aux Laboratoires de l'Institut Scientifique et Technique des Pêches Maritimes, où j'ai passé un séjour depuis la fin du mois de décembre 1955 jusqu'au début de juillet 1956.

Je tiens à remplir un devoir agréable en remerciant sincèrement Monsieur le Professeur R. WEILL, Directeur de la Station Biologique d'Arcachon, et Monsieur P. LUBET Sous-Directeur, qui ont bien voulu m'y accorder l'hospitalité la plus large et m'ont permi d'y poursuivre ces travaux.

Matériel et Techniques

En raison de ces conditions atmosphériques exceptionnelles de février 1956, nous avons faits des déplacements d'inspection pour préciser nos connaissances sur les dégâts causés dans les centres ostréicoles.

De plus, des observations expérimentales ont été faites dans le Laboratoire sur des lots d'huîtres (*Crassostrea angulata* L. et *Ostrea edulis* L.) prélevés quelques jours à la suite des conditions précitées. Ils nous ont servi pour effectuer des expériences sur la congélation, principalement pour étudier d'une manière précise l'action des dits facteurs sur le muscle adducteur.

C'est dans ce but précis et pour obtenir sur le muscle adducteur des renseignements divers d'ordre histologique que nous avons procédé pour faire des coupes à paraffine et à congélation. Dans l'acide azotique à 10%, j'ai trouvé qu'il était assez facile de faire des belles dissociations de muscle. Au contraire, il était difficile de séparer les fibres fraiches.

Dans les cas des coupes à paraffine divers fixateurs ont été employés, mais les fixateurs les plus satisfaisants étaient les mélanges fixateurs alcooliques. Le Bouin alcoolique ou mieux le mélange de Gendre ont été employés avec

Tableau 2

Expérience	Mortalité, % *C. angulata*	Mortalité, % *O. edulis*	Autres observations
1) Un lot d'huîtres plates et un autre d'huîtres portugaises sont exposés à sec à l'extérieure du laboratoire à une température de l'air, maximum −6°C. (minimum −11°C.), et fortement secoués après 18 heures de congélation, puis lentement dégelés.	80	100	Nous avons constaté après dégel lent et complet, que 60% des huîtres portugaises étaient sans réaction, et parmi les huîtres vivantes 50% avaient leurs valves bien fermées tandis que 50% avaient leurs valves ouvertes. Nous avons constaté le décollement du muscle adducteur dans ces dernières, qui étaient donc vouées à une morte certaine.
2) Deux autres lots d'huîtres plates et portugaises sont congelés pendant 18 heures sous les mêmes conditions mais non secoués.	50	100	Nous avons constaté que parmi les huîtres vivantes 100% avaient leurs valves fermées.
3) Un lot d'huîtres plates et un autre d'huîtres portugaises sont soumis à sec à l'extérieure du laboratoire à une temperature de l'air, −8°C., pendant 4 heures de congélation, puis lentement dégelés.	0	100	La durée de cette expérience a été égale au temps normale d'émersion des huîtres sur les parcs de niveaux les plus élevés, soit 4 heures. Nous sommes donc rapprochés aux conditions naturelles.
4) Un lot des naissains d'huîtres portugaises (taille moyenne 8 mm.), congelé pendant 18 heures dans l'eau de mer sous les mêmes conditions comme expérience No. 1.	4	–	Pourcentage plus élevé dans les naissains âgés des huîtres portugaises.

succès. Dans les derniers certains des huîtres congelées (avec leurs valves écartées, et les muscles adducteurs décollés de leurs valves) ont été fixées entièrement. Des autres non-congelées ont été employées comme témoins.

Nous avons fait appel à différents colorants. Des colorations au réactif de Schiff pour la détection de glycogène et des colorations nucléaires à trioxyhématéine ferrique ont été pratiquées.

Pour la détection des matières grasses, des coupes à congélation fixées préalablement au formol salé ont été colorées en bleu. B.Z.L. et les noyaux au carmin alune et montées au sirop de lévulose.

L'Ampleur de Mortalité causé par le Gel et les Excitations Mécanique (Tempête et Brassages)

(a) Observations au nature

A la suite des conditions atmosphériques mentionnés ci-dessus, nous avons fait des déplacements d'inspection dans la région de Marennes-Oléron, centre ostréicole le plus important. Les naissains sur des collecteurs divers et les huîtres adultes dans plusieurs parcs et claires ont été examinés sur place pour déterminer d'une manière plus précise l'ampleur du désastre causé par les grands froids, le gel et la tempête. Le Tableau 1 montre en bref les résultats que nous avons obtenus.

(b) Observations expérimentales

Des expériences ont été faites au Laboratoire pour examiner l'influence du gel et des excitations mécaniques (brassages) sur les naissains et les adultes des huîtres portugaises (*Crassostrea angulata*). Afin de pouvoir comparer l'efficacité des mêmes facteurs précités chez *Ostrea edulis*, j'ai été amené d'effectuer une autre série d'expériences sur les huîtres plates. Le Tableau 2 indique nos expériences et les résultats obtenus.

Dans les tableaux précédants nous avons exprimé la mortalité en pourcentage ceci permettant une comparaison plus facile. Ces résultats (obtenus par l'examen de plusieurs centaines d'huîtres) démontrent clairement que les fortes gelées et les tempêtes sont parmi les grands risques auxquels l'huître est exposé durant sa vie. D'une façon générale, il est possible de remarquer que les pourcentages de mortalité chez l'huître plate étaient toujours supérieurs à ceux de l'huître portugaise. D'après nos résultats expérimentaux une forte gelée prolongée peut réduire le rendement de l'huîtres portugaises à 50% et de l'huîtres plates à 100%. Les pertes sont augmentées de beaucoup par les excitations mécaniques des huîtres congelées pour atteindre chez l'huître portugaise 80% et chez l'huître plate 100%. Dans les claires et les bassins où les huîtres se reposent aux fonds, toujours submergées et donc non prises par le gel, les pertes sont presque nulle.

D'autre part, nos observations condensées dans ces tableaux nous montrent également d'une manière précise l'intervention du muscle adducteur. Nous avons trouvé que toutes les huîtres, qui étaient mortes après la congélation, avaient leurs valves ouvertes. Dans celles qui ont été exposées aux tempêtes (dans les parcs), ou aux brassages (aux laboratoires), nous avons constaté le décollement du muscle adducteur au niveau de son insertion avec la valve supérieure.

Nous allons maintenant examiner la structure du muscle adducteur dans les huîtres congelées et non-congelées, ce qui nous permettra de mieux connaître l'importance du rôle que joue ce muscle dans le phénomène de la mortalité provoquée par de fortes gelées. Il nous permettra, d'autre part, d'étudier les moyens nécessaire pour réduire au maximum les causes des désastres, pour arriver à une plus grande sûreté dans le rendement de l'exploitation au cas d'un hiver rigoureux.

Structure du Muscle Adducteur

(a) Chez les huîtres non-congelées

Chez les huîtres (*Crassostrea angulata* et *Ostrea edulis*), le muscle adducteur est composé de deux parties, l'une blanche et nacrée, l'autre grise et vitreuse; ces deux parties different au double points de vues de la structure et des fonctions.

J'ai étudié l'histologie de ces parties avant et après congélation sur des muscles fixés et dissociés dans l'acide azotique à 10% pendant quelques jours sur des coupes à paraffine et à congélation.

Dans les muscles non-congelés, fixés et dissociés, la partie nacrée est constituée en fibres lisses d'un diamètre oscillant entre 20 et 30 μ et d'une longueur d'au moins 1·25 à 1·75 mm. A part de ces fibres d'un diamètre assez considérable,

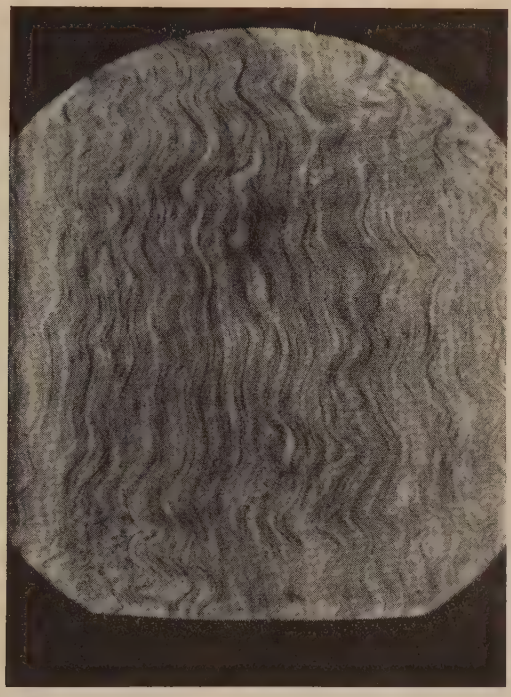

Figure 1. Coupe longitudinale du muscle adducteur de l'huître portugaise (*Crassostrea angulata*), non congelée montrant l'élasticité des fibres musculaires. (Agrandissement $\times 250$).

il en existe d'autres, mais dans un nombre moins grand, ayant seulement 8 à 10 μ de diamètre. Ce sont vraisemblablement de jeunes fibres dont le développement amènera du muscle en épaisseur.

La partie vitreuse du muscle adducteur est formée de fibres ayant un aspect et une structure bien différents. Le diamètre de ces fibres est en moyenne 7 μ et leur longueur atteint 0·90 mm. Certaines de ces fibres s'insertent sur les valves par l'une de leurs extrémités qui sont divisées en deux ou en trois parties obliquement tronquées, les autres extrémités qui se terminent librement au sein du muscle ont une forme conique très longuement effilée. D'autres fibres sont complètement comprises dans l'intérieur du muscle et ont la forme de fusceaux à extrémités très longuement effilées.

En examinant les fibres musculaires de deux parties à un fort agrandissement, on a constaté que leur substance contractile est constituée par des fibrilles parallèles très fines, plus ou moins allongées parallèlement à l'axe de fibre correspondant. Elles sont entourées par un sarcolemme très nettement observable dans les places ou cette membrane fine s'est parfois détachée de la masse fibrillaire. Les fibrilles occupent toute l'épaisseur de la fibre et s'anastomosent entre elles de façon à former une sorte de réseau, à mailles linéaires assez allongées dans la partie nacrée, ou losangiques bien limitées dans la partie vitreuse.

Les fibres de la partie nacrée renferment chacune plusieurs noyaux ovulaires très petits, situés en dehors de la substance contractile sous le sarcolemme et entourés d'une petite quantité de sarcoplasme. Celles de la partie vitreuse renferment chacune un seul noyau petit et ovulaire. Il est situé dans la partie moyenne de la fibre sous le sarcolemme et également entouré d'une petite quantité de sarcoplasme.

Quant au type des fibres constituant la partie vitreuse (lisses ou striées?), c'est une question très discutée, car les différents auteurs sont loin d'être d'accord sur la structure fine de cette partie. D'une façon générale (et à partir des cas rares signalés par SCHEER (1948) chez le *Pecten* et le manteau des Cephalopodes, et par FISCHER (1950) chez les Nudibranches et les Cephalopodes) il est évident que chez les mollusques, les muscles sont surtout formés de fibres lisses remarquables par la lenteur et la puissance de leur contraction. L'allure lente que l'on constate généralement dans les mouvements de ces animaux se rapporte à cette particularité.

Quant aux Pélycépodes, certains auteurs ont signalé que les mollusques qui ont des mouvements très vifs — comme par exemple le battement des valves des Lamellibranches nageurs — les muscles ne sont pas toujours formés de fibres lisses. Ils font remarquer que chez les Monomyaires (*Ostrea*, *Pecten*, etc.), la partie blanche nacrée est formée de fibres lisses aux contractions lentes et soutenues, tandis que l'autre, grise vitreuse, plus ou moins apparente au muscle strié qui présente des contractions rapides et peu soutenues.

D'autres auteurs — dans leurs travaux sur la structure et le mode de contraction des muscles adducteurs des Lamellibranches — ont noté que chez l'huître la partie dite nacrée est constituée en fibres lisses, mais les mêmes auteurs ont fait remarquer que le mode de contraction du muscle adducteur de l'huître, continué par une sorte de tétanos complet, s'approche beaucoup plus à celui du raccourcissement des muscles striés des vertèbres qu'à celui des muscles lisses chez ces animaux.

Les observations de COUTANCE et de BLANCHARD sur l'huître, le *Cardium*, la moule et des autres bivalves, ont au contraire montré que la différence histologique constatée chez le *Pecten* est un fait isolé et que chez les autres bivalves, les portions translucides et opaques des muscles adducteurs sont toutes deux constituées par des fibres lisses un peu différentes d'aspect, mais sans trace de striation transversale.

Nos observations ont montré que les fibres de la partie nacrée sont nettement d'un type lisse. Quant aux fibres constituant la partie vitreuse, leur examen lorsque les tissues sont encore vivantes, n'a montré aucune striation. Il m'est impossible de la distinguer aussi par l'examen sur des pièces fixées et dissociées dans l'acide azotique, ou sur les coupes à paraffine. Il faut noter, que dans ces derniers cas l'action des agents chimiques employés (surtout l'acide azotique, l'acide acétique, et l'acide picrique), détruisent plus ou moins vite la biréfringence, ce qui rend le problème beaucoup plus difficile. Sur les pièces fixées, puis colorées par le trioxyhématéine ferrique, on a mieux pu étudiér la structure du noyau, on a même reconnu que chaque noyau renferme un suc nucléaire abondant au sein duquel se montrent des nucléoles peu nombreuses teintées par la matière colorante, mais sans distinguer encore aucune striation dans les fibres constituant la partie vitreuse du muscle.

Comme déjà indiqué, les deux parties ne fournissent pas la même somme ou genre de travail, et les différences de structure que nous venons de signaler

Figure 2. Coupe longitudinale du muscle adducteur de l'huître portugaise congelée montrant le déchirement des fibres musculaires. (Agrandissement ×150).

peuvent être partiellement attribuées à des différences dans l'état physiologique des fibres correspondantes. D'autre part, la contraction modifie sensiblement la structure physico-chimique des fibrilles. Ces modifications se traduisent quelquefois dans les fibrilles du type strié par un déplacement de la substance colorable des disques épais qui produit l'inversion de la striation en passant par un stade intermédiaire homogène.

(b) Chez les huîtres congelées

L'examen des pièces fraiches prélevées des muscles adducteurs des huîtres préalablement congelées pendant 18 heurs puis lentement décongelées, nous montre que celles-ci, sous pression, laissent échapper une partie notable de leur suc musculaire. C'est causé par une dénaturation qui consiste en une modification irréversible de la structure de protoplasme dont les constituants colloidaux ne possèdent plus la possibilité d'absorber l'eau et de se gonfler.

Figure 3. Coupe longitudinale du muscle adducteur de l'huître portugaise congelée montrant le déchirement et le décollement des fibres musculaires. (Agrandissement ×300).
a. Partie déchirée. b. Niveau de décollement.

D'autre part, l'examen des fibres musculaires sur des pièces dissociées nous montre clairement, qu'elles ont perdu leur élasticité et leur fermeté pour devenir très friable, elles se déchirent facilement. Les mêmes constatations ont été faites par une comparaison portée sur les coupes à paraffine des huîtres non-congelées et celles des huîtres congelées (Figs. 1, 2). On a aussi constaté, que les fibres musculaires ont été moins déchirées chez les huîtres non excitées par rapport à celles des huîtres excitées. Le déchirement, que l'on constate dans les fibres musculaires des huîtres non-excitées, est simplement du à l'action de glaçons formés dans ces tissues. Les excitations mécaniques par suite de l'action de l'homme (brassages pendant leur manipulation), ou de causes naturelles (tempêtes), augmentent d'une part le nombre de fibres déchirées, et d'autre part elles causent le décollement du muscle au niveau de son insertion avec les valves (Fig. 3). Ceci est confirmé par nos observations indiquées dans les tableaux ci-dessus.

On sait que la fermeture rapide des valves est uniquement due à la contraction du muscle vitreux, la partie nacrée fonctionne, grâce à sa tonicité et son élasticité pour équilibrer la force élastique du ligament pour maintenir la fermeture des valves, mais cependant pas d'une façon complète car la partie vitreuse doit contribuer à une faible partie au maintien de la fermeture.

Le déchirement en deux parties des fibres musculaires, en glaçant, est

responsable, soit à relentir, soit à cesser leurs fonctions. En touchant le manteau la valve supérieure ne s'abaisse jamais aussi brusquement jusqu'à l'occlusion complète de la coquille comme avant la congélation. Quelquefois, elle s'abaisse mais très lentement, et la période nécessaire pour la fermeture complète varie selon la durée du congélation. Bien que certaines parmi les huîtres excitées semblaient vivantes aprés leur dégel, car leur manteau se retracte en touchant son bord, celles-ci sont vouées à une morte certaine plus tôt ou tard par l'envasement et l'ensablement.

Depuis longtemps les ostréiculteurs ont remarqué que les huîtres touchées par le froid meurent au bout de trois ou six semaines. C'est-à-dire, les effets du froid ne sont pas toujours immédiatement apparents, ils ne se manifestent souvent qu'à longue échéance.

La détection de glycogène et de matières grasses contenues dans les muscles congelés nous montrait, qu'elles sont fort réduits par rapport à celles existant dans les muscles non-congelés.

Conclusion

D'après l'étude entreprise en février 1956, dont le compte-rendu a été donné sous forme de tableaux, il est évident que:—

1. Les huîtres sont extrêmement sensibles aux grands froids. Les huîtres plates, cependant, sont beaucoup plus sensibles que les huîtres portugaises, celles-ci peuvent supporter une congélation d'une durée de 18 heures.

2. Les naissains résistent bien aux gelées, mais les chiffres de récolte ne cessent de diminuer à cause des autres facteurs qui interviennent pendant la durée du séjour des collecteurs dans l'eau. Il est possible de remarquer, que les coquilles de chapelets et les pierres collecteurs sont éclatés sous l'action du gel prolongé, ils pèlent, les naissains se séparent et sont perdus (par dispersion, envasement et ensablement).

3. Les tempêtes agissent non seulement par la destruction, dispersion, envasement et ensablement des installations de collecteurs, mais les huîtres gelées sont aussi, au moment de la tempête, brassées par les vagues ou les glaçons, et les chocs peuvent occasioner une séparation du corps du mollusque des valves et par conséquent augmenter dans des proportions notables les taux de la mortalité chez les huîtres gelées.

4. Les manipulations violantes ou les brassages par suite de l'action de l'homme, comme la tempête, peuvent augmenter de beaucoup plus les pertes (causées principalement par le déchirement et le décollement du muscle adducteur). Par conséquent, quand les huîtres sont prises par le gel, il ne faut pas les manipuler.

5. Dans les parcs hauts où poussent les huîtres, a marée descendante, l'eau s'est gelée. Puis à marée montante la glace se rompe et les huîtres jettent les glaçons de leur coquilles. Puis la marée descende et la glace se réforme. Les huîtres résistent à ce manège cinq ou dix fois même, puis elles meurent.

Il semble donc fort utile que au cas de grands froids, il ne faut plus laisser geler les huîtres dans les parcs. Par repêchage elles peuvent être entreposées dans les bassins ou les claires. Dans les claires elles gardent une condition excellente et peuvent être protegées du gel ou d'un hiver rigoureux.

Résumé

En raison de conditions atmosphériques exceptionnelles de février 1956, nous avons fait des déplacements d'inspection et des observations expérimentales pour préciser nos connaissances sur la mortalité provoquée chez les huîtres prises par le gel, et l'ampleur de dégâts dans les centres ostréicoles.

D'après les résultats obtenus, une forte gelée peut réduire en 50% le rendement de l'exploitation chez l'huître portugaise, et chez l'huître plate en 100%.

Le phénomène du mortalité provoquée par les fortes gelées est du à la destruction du muscle adducteur, causeé principalement par le déchirement des fibres musculaires.

Les excitations mécaniques par suite de l'action de l'homme (brassages pendant leur manipulation), ou de causes naturelles (tempêtes), augmentent d'une part le nombre de fibres déchirées, d'autre part elles causent le décollement du muscle au niveau de son insertion avec les valves. Par conséquent, les pertes sont augmentées de beaucoup plus pour atteindre 80% chez les portugaises, et 100% chez les plates.

Pour réduire au maximum les causes de désastres au cas d'un hiver rigoureux, il faudra repêcher les huîtres des parcs avant qu'elles ne gèlent et les mettre dans des bassins ou des claires où elles gardent une condition excellente. Quand les huîtres sont déjà prises par gel, il ne faut pas les manipuler.

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Essay Review
Some Recent Studies of Oceanic Circulation

By

K. F. Bowden

The following papers are covered in this review:—

(1) **K. Hidaka.** "A theoretical study on the general circulation of the Pacific Ocean." Pacific Science, **9**: 183–220, 1955.
(2) **J. G. Charney.** "The Gulf Stream as an inertial boundary layer". Proc. Nat. Acad. Sci., **41**: 731–740, 1955.
(3) **G. W. Morgan.** "On the wind-driven oceanic circulation." Tellus, **8**: 301–320, 1956.
(4) **J. C. Freeman, Jr.** "Note on a prediction equation for the surface layer of a two-layer ocean." Trans. American Geophys. Union, **35**: 585–587, 1954.
(5) **J. G. Charney.** "The generation of ocean currents by wind". J. Mar. Res., **14**: 477–498, 1955.
(6) **G. Veronis** and **G. W. Morgan.** "A study of the time-dependent wind-driven ocean circulation in a homogeneous, rectangular ocean". Tellus, **7**: 232–242, 1955.
(7) **G. Veronis** and **H. Stommel.** "The action of variable wind stresses on a stratified ocean". J. Mar. Res., **15**: 43–75, 1956.
(8) **G. Veronis***). "Partition of energy between geostrophic and non-geostrophic oceanic motions." Deep-Sea Res., **3**: 157–177, 1956.
(9) **A. B. Arons** and **H. Stommel.** "A β-plane analysis of free periods of the second class in meridional and zonal oceans." Deep-Sea Res., **4**: 23–31, 1956.

One of the major problems of oceanography is the relation of the circulation of the oceans to the wind systems acting on their surface. It is now generally accepted that the chief features of the mean circulation in the upper layers are due, directly or indirectly, to the wind stress. It is less certain to what extent the influence of the winds affects the deeper layers or how the circulation as a whole responds to changes in the winds.

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*) See also J. du Cons., **23** (2): 301–02.

The foundation of a theory of the wind-driven circulation was laid by Ekman in 1905. He introduced two important concepts: the fundamental significance of the earth's rotation and the transmission downwards of the wind's stress on the surface by shearing stresses in the water, characterized by an eddy viscosity several orders of magnitude greater than the molecular viscosity. In the case of a wind blowing uniformly over an ocean of infinite extent, Ekman showed that the surface would remain horizontal and the currents would be confined to a shallow surface layer, of the order of 100 m. thick. As soon as one introduces coastal boundaries to the ocean, or allows the wind stress to vary from one part of it to another, this result is modified. The water becomes piled up in some areas and depleted in others and the surface slopes give rise to horizontal pressure gradients, which in turn produce currents extending, in the case of an ocean of uniform density, to the bottom. Ekman gave solutions for a number of problems involving a homogeneous ocean. In an actual ocean, in which the density increases with depth, it is possible for the surfaces of equal density to become inclined to the isobaric surfaces in such a way that, below some depth, the horizontal pressure gradients are reduced to zero. Observations show that the velocities of the mean part of the wind-driven circulation fall to very small values at a depth of several hundred metres, and it is deduced that such an adjustment of the density distribution does, in fact, occur. Considerable mathematical difficulties arise when one attempts to extend Ekman's theory to an ocean in which the density varies with depth.

Sverdrup, in 1947, showed that by working in terms of the mass transport, integrated from the surface to the depth at which the horizontal pressure gradients vanish, one could relate the transport of the currents to the wind stress, without having to take into account the actual variation of density and of shearing stress with depth.

A remarkable feature of the actual oceanic circulation is the lack of east-west symmetry in the flow. On the western side of an ocean an intense current is developed, e. g., the Gulf Stream or the Kuroshio, which has no counterpart on the eastern side. Stommel showed, in 1948, that this westward intensification is due to the variation of the Coriolis parameter with latitude. This parameter, usually denoted by f, is equal to 2ω sine φ, where ω is the angular speed of rotation of the earth and φ is the latitude. It may be described as the vertical component of the vorticity (or spin) of an element of water due to the rotation of the earth.

In Ekman's theory, the steady-state circulation was envisaged as being in equilibrium between the energy supplied at the surface and that dissipated by friction at the bottom. Since the wind-driven currents in the real ocean do not extend to the bottom, it seems unlikely that bottom friction can be the dissipating mechanism. Rossby suggested, in 1936, that lateral stresses, originating at the coasts and being transmitted to the interior of the ocean by horizontal eddy viscosity, could provide the balance. Munk combined the variation of the Coriolis parameter with the concepts of an integrated mass transport and of lateral shearing stresses and was able, in 1950, to develop a theory which reproduced the main features of the average wind-driven circulation in all the oceans. Similar work was carried out by Hidaka and others.

At this stage a theoretical framework had been evolved which appeared to account satisfactorily for the large-scale features of the wind-driven circulation

in its steady state. A number of questions remained unanswered, however. By working with mass transports one can avoid considering how the currents vary with depth, but the depth to which appreciable current velocities extend is itself an important question. Although the introduction of the variable Coriolis parameter has reproduced the westward concentration of flow as an essential feature, it does not account adequately for the intense jet-like character of the Gulf Stream or Kuroshio. Moreover, the mechanism by which the energy supplied to the ocean by the wind is being dissipated is uncertain. Bottom friction is an unlikely explanation; lateral friction is possible but requires numerical values of the lateral eddy viscosity of the order of 10^8 cm^2./sec., which seem too high, unless one regards the large-scale meanders of the Gulf Stream, for example, as dissipating eddies.

Another question is how the circulation may be expected to respond to changes in the wind stress, whether of a transient or periodic character. Rossby, in 1938, considered the effect of varying wind stress on a stratified ocean, and concluded that currents extending to the bottom would be produced, even when the rate of variation was very slow. This result was surprising, in view of the observed restriction of the steady part of the flow to a limited depth, but appeared to be theoretically unassailable. If varying wind stress due, for example, to the passage of a succession of storms, can produce random currents in the deeper layers, then, as pointed out by Sverdrup, these will have the effect of a large lateral eddy diffusivity. Thus the possibility exists of a variable wind stress on the surface influencing the movements and properties of the deep and bottom water masses.

This is the background to the theoretical studies which are under review. The first three papers listed above deal with the response of the ocean to a steady distribution of winds, while the others are concerned with the effects of wind systems which vary with time.

The paper by Hidaka (1) is an extension of his earlier work on the circulation of the Pacific Ocean, in which he calculated the integrated mass transport produced by a distribution of winds, varying with latitude in accordance with observations. In this paper Hidaka sets out to calculate the vertical distribution of velocity, thus including both vertical and lateral eddy viscosity terms in the equations of motion. The vertical eddy viscosity A_z enters in the form of a depth $D_z = \pi\sqrt{A_z/\varrho\omega}$, analogous to Ekman's "depth of frictional influence". The Pacific is approximated by a square ocean, extending from 60° N. to 60° S. and through 120° in longitude. The water is assumed to be of uniform density and infinite depth. By treating the problem in three dimensions instead of two, the calculations are complicated enormously. Numerical results have been obtained for the streamlines over the western part of the ocean, at the surface and at depths 0·5, 1, 1·5, 2, and 3 times D_z. The surface pattern of flow corresponds fairly closely to that found previously for the mass transport. Comparing the calculated velocities with those observed in the fastest part of the Kuroshio, Hidaka deduces that the best agreement is obtained by taking $D_z = 75$ m., corresponding to $A_z = 422$ gm.cm./sec. At the subsurface depths, the pattern of flow does not change greatly from that at the surface, the velocity falling off comparatively slowly with depth.

It would be easy to question the validity of the various simplifying assumptions, such as the neglect of any density structure and the uniformity with depth of the vertical eddy viscosity. A more fundamental point is that Hidaka's

treatment assumes the vertical component of velocity to be negligible everywhere. As STOMMEL and CHARNEY have pointed out, the vertical velocities at the base of the EKMAN layer, although small in absolute magnitude, may be regarded as the chief way in which this layer affects the deeper layers of the ocean. HIDAKA's investigation is valuable in showing that the mass transport method, reducing the problem to two dimensions, leads to a pattern of flow which is not basically different from that taking some account of the vertical structure of the currents.

The remaining papers have certain common features in their approach and in the mathematical models adopted to formulate their problems, and it is convenient to consider these features collectively. In many cases, a two-layer ocean is postulated, the density being uniform in each layer with a discontinuity at the interface. It is assumed that no frictional stress can be exerted across the interface, so that motion in the lower layer must be due entirely to pressure forces transmitted to it from above. When numerical values are taken to approximate to the Atlantic Ocean, the upper layer is taken as being 500 m. thick, the lower 3,500 m. and the discontinuity in density as 2×10^{-3} gm./cm^3. The two layers thus correspond to the water above and below the main thermocline. The two-layer model, although admittedly a very rough approximation to the real, continuously stratified ocean, can be expected to disclose those features of the flow which depend essentially on its stratified character.

Since the authors are concerned with the average currents, or the vertically integrated transports in each layer, they exclude at the outset any consideration of the details of the flow in the frictional layer near the surface. This layer is regarded simply as an intermediate stage in transferring momentum from the wind to the flow in the upper layer as a whole. In this respect the wind stress may be regarded, as CHARNEY (5) has discussed in some detail, as a body force distributed uniformly throughout the depth of the upper layer.

In a two-layer ocean, the possible motions may be classed as barotropic or baroclinic. In a barotropic mode of motion the ocean responds in essentially the same way as if it were homogeneous. The interface between the two layers is hardly disturbed, horizontal pressure gradients are effective throughout the depth and the average velocities are similar in the two layers. The Ekman spiral velocity distribution is understood to be superimposed in the upper part of the upper layer, although it is not explicitly considered. In a baroclinic mode, on the other hand, movement of the interface plays an essential role. Its slope is many times greater than that of the free surface, in a ratio which is of the order $\varrho/\Delta\varrho$, where ϱ is the mean density and $\Delta\varrho$ is the increment of density across the interface, and is in the opposite sense, so that the horizontal pressure gradients are reduced. The velocities in the lower layer are, therefore, much smaller than those in the upper layer.

From another point of view, the possible motions, whether barotropic or baroclinic, may be described as geostrophic or non-geostrophic. In geostrophic flow, the horizontal pressure gradients are balanced by the Coriolis acceleration and the water has no acceleration relative to the earth. If such a balance is approximately maintained, the flow is known as quasi-geostrophic. When the balance is more or less incomplete, the accelerations cause oscillatory motions, often termed inertio-gravitational waves, to occur. As mentioned earlier, it is a fact of observation that the steady-state circulation of the actual oceans is

predominately baroclinic and geostrophic, and this feature should emerge from any theory purporting to represent the flow.

The variation of the Coriolis parameter, $f = 2\omega$ sine φ, with latitude would be incorporated automatically in a treatment of oceanic movements on a "rotating sphere" model of the earth, but is lost if the equations of motion are simplified to those of a "rotating plane" model, unless deliberately retained. For greater ease in mathematical manipulation, it has become customary to treat the circulation in plane co-ordinates, but to take the Coriolis parameter as varying linearly with latitude. Thus if the x-axis is taken towards the east and the y-axis along a meridian towards the north, the variation of the Coriolis parameter is df/dy, which is denoted by β and regarded as a constant. This procedure defines the β-plane of ARONS and STOMMEL (9).

In paper (2), CHARNEY starts with MUNK's theoretical treatment of the general circulation in the North Atlantic and considers in detail the formation of an intensely narrow current, corresponding to the Gulf Stream, at the western boundary. In the central part of the ocean, a balance exists between the wind stress, the pressure gradients, and the Coriolis acceleration. In the western current, CHARNEY assumes that the direct effect of wind stress on the surface is negligible, but that a balance exists between the pressure gradients, the Coriolis acceleration, and the field-acceleration terms. These terms are those of the form $u\partial u/\partial x$, arising from the change of velocity with position in the pattern of flow. Such accelerations are small in the open ocean, but become large as the current approaches the coast. The Gulf Stream is thus regarded as an inertial reaction of the water near the coast to the westward transport of water from the centre of the ocean. The variation of the Coriolis parameter plays an essential part in the formation of the narrow boundary layer current.

On the basis of a two-layer ocean, with the current confined to the upper layer, CHARNEY has computed the contours of depth of the upper layer, the streamlines and hence the velocity distribution, and obtains moderately good agreement with the observed values. An interesting feature of the theory is that it predicts that the separation of the flow from the coast should start at a point halfway from the Strait of Florida to Cape Hatteras, irrespective of the presence of a protrusion, such as actually occurs there. Since lateral shearing stresses are neglected, there is no dissipation of energy in this model of the Gulf Stream, and the velocity increases to a maximum at the western edge of the current. To provide for the dissipation of energy, a frictional boundary layer might be introduced between the inner edge of the inertial boundary layer and the coast.

MORGAN, in paper (3), makes a new approach to the general problem of the wind-driven circulation in an enclosed ocean in its steady state. To avoid the pitfalls of projecting the motion prematurely on to a plane, he develops the equations of motion on the rotating earth in spherical co-ordinates, for the two ideal cases of a homogeneous and a two-layer ocean. From an analysis of the orders of magnitude of the various terms in the equations, he proposes an ocean model consisting of three regions. Referring to the North Atlantic, between 10° N. and 50° N., the ocean is divided into a northern and a southern region by latitude 35° N. The southern part is subdivided into a broad, central and eastern part and a narrow part near the western boundary. In the broad region, only the wind stress, pressure gradients, and Coriolis acceleration are

important, while in the western region a boundary layer flow develops, dominated by the non-linear field-accelerations and the Coriolis parameter, varying with latitude. Frictional forces are assumed to be negligible in both these regions. Morgan points out that some dissipating force, probably lateral friction, must be effective at some stage in the circulation, but this is relegated to the third region, corresponding to the Gulf Stream north of Cape Hatteras. The remainder of the paper is devoted to the solutions of the equations for the first two regions only.

Morgan obtains solutions for a homogeneous and a two-layer ocean, with a distribution of easterly winds over the first region, their speed falling to zero at its northern boundary. The analysis shows that the variation of the Coriolis parameter is fundamental in the formation of a narrow stream near the western shore and that no similar stream can be formed on the eastern side. This is true for both the homogeneous and two-layer oceans and it is concluded that density stratification acts as a modifying factor, rather than a fundamental one, in the formation of the western current. Morgan's treatment of the flow in his second region resembles Charney's boundary layer theory of the Gulf Stream, derived independently.

Freeman's paper (4) has the limited objective of finding an equation for predicting the change in depth of the thermocline due to an applied wind stress. He considers the response of a two-layer ocean to a wind stress which varies with position across it. In the northern hemisphere, the wind produces a transport of water to the right of its direction and proportional to its stress. If a region of weak winds exists to the right of a region of strong winds, for example, this will tend to result in an accumulation of water in between the two regions, leading to an increase in the thickness of the upper layer. By making rather drastic assumptions about terms which can be considered negligible in the equations of motion, Freeman derives an equation for the rate of change of depth of the upper layer in terms of the horizontal variation of the wind stress.

In (5) Charney considers the development of large-scale oceanic currents by winds which change with time. Provided the time-scale is long compared with half a pendulum day (= 12 hours/sine φ), it may be assumed that most of the energy communicated to the sea by the wind goes into motions which are, at least approximately, in geostrophic balance. Equations applicable to quasi-geostrophic motions are developed and then applied to particular problems. Two of these deal with a wind stress applied to a finite strip of an infinite ocean, initially at rest, when the Coriolis parameter is assumed constant. These problems are similar to ones treated by Rossby in 1938 and essentially the same results are obtained. In a two-layer ocean, the response depends on the width of the strip. If it is 100 km. wide, the motion is mainly baroclinic, with a large change in the slope of the interface and much reduced velocities in the lower layer. If the width is 1,000 km., the barotropic mode predominates, i. e., the motion is practically independent of depth, except near the edges of the strip, where the baroclinic effects become large. This result suggests that a coastal boundary might favour the baroclinic response, even in the absence of variation of the Coriolis parameter. Investigating this point further, Charney finds that, although the baroclinic part of the flow would be small away from the coast, it would predominate within a distance of the order of 30 km. from it.

Taking the variation of the Coriolis parameter into account, it is found that a travelling wind system, moving very slowly (with a period of the order of 8 years) would cause a response which was mainly baroclinic. CHARNEY does not, in this paper, extend the investigation to an ocean enclosed by boundaries.

VERONIS and MORGAN (6) consider the circulation due to winds which vary sinusoidally in velocity about their mean values. Their model is a rectangular ocean with easterly winds over its central part and westerlies over the northern and southern parts. The general character of the problem, except for the variability of the wind stress, is similar to that treated by MUNK. The solution gives the variation in mass transport of the currents, their phase lag behind the wind and the contours of the surface elevation. Numerical values are taken to approximate to the Atlantic Ocean with a yearly period of variation. The wind directions are assumed to remain constant while the stresses vary in the range $\pm 20\%$ of their mean values. The general pattern of flow appears to change little during the yearly cycle. No appreciable variation in the position of the Gulf Stream, for example, is indicated. The magnitude of the mass transport varies by an amount of the same order as that of the wind stress variation. The time by which the phase of the transport lags behind that of the wind is found to be independent of the frequency of variation: it is 3 days in the centre of the Gulf Stream and $4\frac{1}{2}$ days in the counter-current on its eastern side.

In (7), VERONIS and STOMMEL carry out a general investigation into the response of the ocean to variable wind stresses. They consider a two-layer ocean which is infinite in extent but the wind systems are taken to be of finite dimensions. The main points of interest are whether the currents induced by the wind are confined to the upper layer or extend throughout the whole depth of the ocean, and whether the slope of the interface responds to the wind or remains virtually unaffected. The variation of the Coriolis parameter is taken into account and the equations of motion in the two layers are treated in such a way that the normal modes of motion are evolved. The free waves which are possible in the ocean, corresponding to the normal modes, are of six types. One pair of modes represents motions which are in geostrophic balance and correspond to the currents normally measureable in the ocean. One mode of this pair is barotropic and the other baroclinic, these terms having the meanings discussed above. These two free motions are commonly called "planetary waves" or "Rossby waves" and can travel only from east to west. They have periods ranging from a few days up to several years. The other four types of wave arise from a lack of balance between the pressure forces and the Coriolis acceleration and have periods less than, or approximately equal to, half a pendulum day. One pair is barotropic, corresponding to long gravity waves, travelling with a speed $\sqrt{gh}$, where h is the total depth of the ocean (for very long waves the velocity is modified due to the earth's rotation). The other two are baroclinic, corresponding to long internal waves travelling at much slower speeds. They become inertial motions when the period approaches its limiting value of half a pendulum day. One wave of each of these two pairs travels towards the east and the other towards the west, and the earth's rotation affects their velocity of propagation differently.

Two problems involving variable wind stresses are then considered. The first concerns a moving pattern of northerly and southerly winds, corresponding

to the passage eastwards of a series of atmospheric ridges and troughs. It is found that the nature of the response of the ocean depends on the period of the passing wind systems. For periods of one to seven weeks, the ocean responds mainly as a homogeneous body of water, the currents extending to the bottom. The baroclinic effect becomes more important as the period increases, but even for a period of a year the barotropic response is comparable with it. Only when the period approaches 100 years are the currents confined to the upper layer.

The second problem concerns a wind stress which is applied for a limited time only, comparable with the life of a storm. It is found that, as long as the wind blows for more than half a pendulum day, most of the energy goes into the geostrophically-balanced flow. The flow is partly barotropic and partly internal, the proportion depending on the scale of the motion. Thus the barotropic effect increases as the scale becomes larger, as found by Charney (5). The movement of the thermocline may be 10 to 20 m. for a wind blowing for 3 days and thus be quite measurable. It is concluded that the currents in the lower layer will be small (not more than 1 cm./sec.) and unlikely to produce a mechanism for large-scale lateral mixing, as suggested by Sverdrup in 1939. Veronis and Stommel discuss the application of their model to a real, bounded ocean and conclude that the model should correspond essentially to a real ocean for a storm lasting, say, 5 days, but that there is some doubt of its applicability for periods of several weeks.

In (8), which is an extension of the previous work, Veronis deals with the response of the ocean to a wind stress applied to it for a period of a few hours only. The solution is found in terms of the normal modes, as above, and numerical results are given for the case of wind acting on a strip, 200 km. wide, of a two-layer ocean. A given amount of momentum is taken as being imparted (a) impulsively, (b) during an interval of 6 pendulum hours, (c) during 12 pendulum hours. The proportion of energy going into the inertio-gravitational wave motions is (a) 74%, (b) 51%, and (c) 11% in these three cases. Thus when the momentum is added for half a pendulum day, 89% of the energy goes into geostrophic flow. The inertial motions are almost entirely internal, with a period of half a pendulum day, and are propagated away from the source region with the slow speed characteristic of internal waves: about 3 m./sec. in this case. In the later stages, only the geostrophic flow remains. From a practical point of view, the results indicate that the maximum change in the depth of the thermocline would be about 3 m. for a wind stress of 3 dyne/cm^2. acting for 12 pendulum hours. The velocities generated in the lower-layer would be very small and unlikely to be detectable.

The importance of the earth's rotation in influencing the natural oscillations of the oceans has been recognized in tidal theory for many years. Oscillations which would be possible, even if the earth were non-rotating, become modified by its rotation. Other types of motion, such as a circulating current, which would be steady on a non-rotating sphere, are converted by the rotation into long-period oscillations, which have been called "oscillations of the second class" to distinguish them from the former type. They correspond to the first normal mode found in the investigation of Veronis and Stommel, discussed above, and their properties are the subject of the paper by Arons and Stommel (9). Because of the mathematical difficulties inherent in the study of oscillations in bounded oceans on a rotating spherical earth, the authors have reduced the

motion to that on a non-uniformly rotating plane: the β-plane. Solutions found in this way will not be exact, but may be expected to exhibit the major features of the motions.

ARONS and STOMMEL demonstrate, firstly, the properties of free, progressive waves which are in quasi-geostrophic balance. These are the planetary, or Rossby waves, having a phase velocity directed always towards the west. Their dispersive properties, however, are such that the group velocity, with which their energy is propagated, may be either eastwards or westwards. ARONS and STOMMEL then consider standing waves of this type, which can be set up in an ocean bounded by meridians. Such a standing wave is formed by two progressive waves of the same period but of different wavelengths, both of westward phase velocity but with group velocities in opposite directions. A number of numerical examples are given. In the North Atlantic the first mode (of shortest period) would have a period of 4·7 days in latitude 30° N. and 9·6 days in 45° N. In the North Pacific the corresponding periods would be 3·0 days in 30° N. and 6·0 days in 45° N. In the case of the Antarctic Ocean, i. e., a zonal ocean encircling the earth, a number of free periods are found, the shortest being 6·75 days with a wavelength of 10,500 km. ARONS and STOMMEL suggest that oscillations of this type might be excited by meteorological forces as well as by tidal forces. Since the waves are barotropic, with currents extending to the bottom, it is possible that they might have a significant effect on the deep water masses.

The papers here reviewed represent an important advance in the theory of ocean currents. Our understanding of the steady, wind-driven circulation has been put on a firmer basis and the relative significance of the various forces acting in different parts of the flow has been clarified. Little work had been done previously on the effects of variable wind stresses, and the introduction of the concept of normal modes of motion into this subject has proved to be a fruitful technique. It may still be possible to argue about whether varying winds on the surface can have an appreciable effect on the movements or mixing of the deep water masses. One of the difficulties here is in judging the extent to which results obtained from the, necessarily idealized, mathematical models can be applied to events in an actual ocean.

One could not end this essay without referring, at least in passing, to a recent paper by STOMMEL*, in which he summarizes and extends much of the work covered in the papers under review. He is able, moreover, to attempt a new synthesis, embracing both the wind-driven and thermohaline circulations. It would be inappropriate, in a review covering a more restricted field, to comment fully on this important paper.

*) H. STOMMEL, 1957. "A survey of ocean current theory." Deep–Sea Res., 4: 149–84.

Reviews

R. P. Dales. "Pelagic Polychaetes of the Pacific Ocean." Bull. Scripps Inst. Oceanogr. Calif., 7 (2): 99–168, 64 figs. and charts. Berkeley & Los Angeles, 1957.

Before the appearance of this paper only very little was known about the distribution of pelagic polychaetes of the Pacific Ocean, our knowledge of the group being mainly restricted to the Mediterranean, the Atlantic, and Antarctic regions. Only few oceanographical expeditions in the Pacific have collected pelagic polychaetes in any great amount, thus a very detailed chart of their distribution is not at present possible. After the present investigation, however, a more detailed account can now be given within the area explored.

The present paper is mainly based on a comprehensive material collected by the Marine Life Research during the first year's cruises (1949–1950) of the M.L.R. programme, but additional information was obtained from other collections made, e. g., by the Hopkins Marine Station and the Office of Naval Research, in Monterey Bay.

The plankton samples taken by the M.L.R. originate from a wide area from Cape Disappointment, Oregon, (about 47° N.) to San Eugenio, Mexico (about 27° N.), a distance of about 3,000 km. and offshore for about 800 km. The investigations were mainly confined to the upper water layers, within 75 m. of the surface, a fact which necessarily must make the idea of not only the vertical range but also the composition of the fauna of pelagic polychaetes rather incomplete, since many of the species are known to be inhabitants of greater depths; this was, however, in some way redressed by the great number of night hauls, for many species undertake rhythmic vertical migrations during 24 hours.

The paper is divided into two chapters. The first one, by far the biggest, is a systematical survey of the pelagic polychaetes occurring in the Pacific; the other is a discussion of their distribution in the area. Here at last there are keys for the identification of genera and species, and it is of great value that these keys include species which occur elsewhere but have not yet been recorded from the Pacific.

Finally there is an exhaustive list of literature on the subject. The drawings are graphical, emphasizing the systematical characters; charts of distribution and curves of currents and temperature over the area studied are given.

Only a few families of polychaetes are genuine pelagic (naturally the pelagic phases during the life cycle have not been considered). Of the Phyllodocidae

only members of the subfamily Lopadorhynchinae were found in the M.L.R. collections (7 species); of the two other subfamilies, Iopsilinae and Pontodorinae, only the genera *Iopsilus* and *Phalacrophorus* are considered on the basis of TREADWELL'S specimens.

All the members of the families Alciopidae, Tomopteridae, and Typhloscolecidae are pelagic, and all easily recognizable. DALES (1955) has discussed the evolution and relationships of the genera of the Alciopidae. The systematics of the Tomopteridae are mainly based on the presence or absence and the situation of the different glands in the pinnules; the author gives a useful survey of the terms of these organs used in descriptions in the English, Italian, and German languages.

No new species are described.

Our present knowledge of the Pacific pelagic polychaetes may be scheduled thus:—

Phyllodocidae.....	7	species	(	5	secured	by	M.L.R.)
Alciopidae.....	20	–	(11	–	–	–	)
Tomopteridae.....	10	–	(3	–	–	–	)
Typhloscolecidae	5	–	(3	–	–	–	)

As regards the species which were not secured by the M.L.R. information come mainly from CHAMBERLIN (Mem. Mus. Comp. Zool. Harvard, **48,** 1919), TREADWELL (Carnegie Inst. Washington, Publ. 555, 1943), ROSA (Boll. Mus. Zool. Anat. Comp. Turino, **23,** 1908; Publ. Inst. Firenze, **1,** 1908), and DALES (Ann. Mag. Nat. Hist., Ser. 12, **8,** 1955).

E. Wesenberg-Lund

J. A. Gulland. "On the fishing effort in English demersal fisheries." Min. Agric. Fish. and Food, Fish. Invest., Ser. 2, **20** (5): 1–41, 24 figs. London, 1956.

Investigations of the problems concerned with the operations of fishing have become increasingly important to fishery biologists in later years mainly because the application of the modern theories of fishing demands more detailed and exact information of these matters. There are therefore special reasons for welcoming this paper which also seems to form the first main contribution to our knowledge of the fishing effort of a large modern trawler fleet.

In the introduction to his paper the author first defines the terms used. The fishing effort of a vessel is thus defined as the product of its fishing power and a measure of the time spent fishing. The fishing power may be defined by reference to a standard vessel by comparing their catches when fishing at the same time and place. When trying to estimate the fishing power of a whole fleet of trawlers, account should be taken of the fishing power of each ship or each category of ship for which the fishing power may be assumed to be constant. It is therefore of great value to study the relation between the fishing power and the various vessel characteristics in order to find a factor readily determined from the specifications of the ship which is proportional to the fishing power, and thus can be used to evaluate the changes in the fishing power of a whole fleet. Other measures of fishing effort which have sometimes been used are per-

formance and fishing capacity. The performance of a vessel is simply defined as its catch per unit of fishing time irrespective of time and place, and the fishing capacity as the gross catch over a period. Performance therefore takes into account the range of the ships, while fishing capacity also includes the ability of some ships to do more fishing during a year than others.

In the chapter on the calculation of the fishing power the methods are discussed in detail. The formal definition by reference to the catches of a standard ship, is actually an attempt to refer to the varying density of fish. But direct measures of fish density are usually not obtainable. Instead of using the catch of one standard vessel as an index of the fish density, it is therefore more practicable to make use of a group of standard ships, the fishing power of which are known. The requirement for such a group of standard ships is that each of the ships in the group should at least once have fished at the same time and place as each of the others. By referring the catch per unit of fishing time of each ship to the corresponding data for the rest of the group an arbitrary measure of the fishing power of each ship in the standard group is obtained. In this way the fishing power can be calculated for groups of standard trawlers operating in different areas such as the Barents Sea, Iceland, the North Sea, and the Irish Sea. The scales, on which the fishing power of these ships are measured, are different, but they differ only by a constant. After having determined the fishing power of the standard ships once and for all, use can be made of these data to find the fish density in areas where standard ships have been fishing, thus providing indices to which the catch per unit of fishing time of non-standard ships can be referred. By this procedure the fishing power of some 450 vessels or approximately 40 per cent. of the English first class demersal fleet was assessed.

An extensive chapter of GULLAND's paper deals with the relation between fishing power and vessel characteristics. It is thought that the most important factors which influence the fishing power of a trawler, are the size of the trawl and the speed at which it can be towed, which depend on the size of the ship and the power of its engines. Gross tonnage is used as a measure of the size of the ships, and the regressions of fishing power on gross tonnage, which are demonstrated for six groups of trawlers, are clearly significant. In the case of the distant water fleet of larger steam trawlers the nature of the relationship between fishing power and gross tonnage was found to be a simple proportionality, thus providing a convenient index of fishing effort, the ton-hour. But for three groups of the smaller vessels of the home fleet the regressions departed significantly from proportionality, the smaller ships being ton for ton the more powerful. A comparison showed that motor trawlers appear to have a greater fishing power than steam trawlers of the same tonnage. In order to obtain a comparable measure of the fishing power for all sizes and types of trawlers an "equivalent tonnage" is defined as being proportional to the fishing power. For steam trawlers over the range 200–750 tons the "equivalent tonnage" is the same as gross tonnage. For the small steam trawlers and for the motor trawlers the "equivalent tonnage" could be determined empirically from the regressions of fishing power on gross tonnage. An analysis of the relation between the fishing power and other vessel characteristics, such as net tonnage, length, and horse power, showed that all of these, as one might expect, were closely related to the fishing power. The data available indicated, however, that gross tonnage was the best measure of those considered. It is

also possible that some of the factors, for instance, tonnage and horse power, may to a certain extent act independently in influencing the fishing power. To study this the partial correlation coefficients between fishing power, gross tonnage, and horse power were calculated for some sets of data. The results suggested that both tonnage and horse power influence the fishing power. The author therefore emphasizes that the "equivalent tonnage" expressed in terms of gross tonnage is a valid measure of fishing power only as long as the power of each size of vessel remains constant. The difference which was found between the fishing power of steam and motor trawlers is thus ascribed to the fact that the motor trawlers have, size for size, the more powerful engines.

GULLAND also comments upon the relation between the fishing power of a trawl and the mesh size. It is known that the fishing power increases with increasing mesh size. Fishing power and fishing effort should therefore always be referred to the mesh size which has been used.

An analysis of the fishing power of seiners showed an important but not unexpected difference from that of the trawlers in that the fishing power appears to be independent of the size of the ships. For catches of all demersal species the average fishing power of some 50 seiners was found to be 160 equivalent steam trawler gross tons, while the same figure for the catch of plaice only was 248. An estimation of the fishing power of pair vessels based on data of eight pairs of trawlers, showed that when it is one of a pair, a vessel of some 200 tons has an equivalent tonnage of about 320 tons. The fishing capacity of both seiners and pair vessels was found to be reduced relative to that ordinary of trawlers because of fewer hours fishing per year.

It would greatly facilitate the calculation of fishing power if performance could be used as an approximation, then the calculations could be based on catch per unit fishing time irrespective of time and place. An analysis of the relation between performance and fishing power for groups of trawlers in two regions, such as Iceland and the North Sea, showed that performance could under certain conditions give a fair estimate of fishing power. A reasonable restriction of the time and place of the data seemed, however, to be necessary.

In a discussion of the best measure of fishing time the author shows that significant errors may be introduced if use is made of days absence from port. If the fishing grounds are far away, the relation between days absence and actual fishing time will thus be influenced by the speed of the ship. Furthermore various forms of vessel saturation may occur. At high fish densities the time spent fishing in order to get a full catch will be less, and the time spent steaming to and from port will accordingly make out a larger part of the days absence. Also, when fishing is very good, the increased time spent in handling the catch will reduce the actual fishing time of each day spent fishing. For these reasons records of hours fishing should always be preferred to days absence, or even days spent fishing.

In a final chapter the effects of using the more refined measures of fishing effort discussed in the paper are demonstrated with data from the English fishery at Iceland and on the Norwegian coast.

GULLAND's paper will no doubt be an incentive for other workers in this field to examine their data in a similar comprehensive and useful way.

G. Sætersdal

P. R. Walne. "Experimental rearing of the larvae of *Ostrea edulis* L. in the laboratory". Min. Agric. Fish and Food, Fish. Invest., Ser. 2, **20** (9): 1–23, 4 figs. and 2 pl. London, 1956.

The author describes a technique of rearing the larvae of *Ostrea edulis* in vessels of 1 litre capacity without change of sea water. With this technique he carried through a great number of experiments in a glass house of the Conway laboratory. It is clear that a far greater number of experiments, involving variation of several factors, can be carried out in a given amount of time by using 1 litre vessels, than was ever possible in using the few big concrete tanks of the Conway station in which so much practical experience on the rearing of oyster larvae has been gained in previous years.

Everyone interested in shellfish biology and shellfish farming will be very grateful that the results obtained have been made available in printed form, for too often such valuable information, especially when difficulties hard to understand are encountered, are put to sleep in the files of a laboratory. And is it not primarily the failures which sooner or later appear to increase our knowledge and insight, rather than immediate success?

Of the approximately 200 feeding experiments made, many have been failures for no apparent reason. Contrary to the former experiments in big tanks, the type and quantity of food used was under strict control. It could be concluded that the suitability as food varies widely from one species of nanoplankton to the other. Relatively few appeared to be very good larval food if used in pure culture (e. g., *Pyramimonas grossii* Parke (Chlorophyceae), *Chromulina pleiades* Parke, and *Isochrysis galbana* Parke (Chrysophyceae). No growth could be obtained with many a nanoplankton form, including thick walled *Chlorococcales*, and some forms (e. g., *Prymnesium parvum* Carter) appeared to be definitely toxic to oyster larvae.

Sometimes even the most successful food gave some failures. As successful and unsuccessful series of experiments often occurred at the same time, or very close together, WALNE is inclined to think that the fault lies with the larvae, rather than with the quality of the food or of the sea water in which the larvae were being reared. He believes that the condition of the parent oysters may greatly influence the vigour of the larvae produced, especially through variation of the amount of food reserve in the larvae when they are liberated. This may be true, but before assuming that this is really the most important reason for failures in the rearing of larvae we should very much like to have figures on the condition index or on the chemical composition of both adult oysters and samples of the newly liberated larvae. It is certainly not impossible that a correlation between condition and vigour might be found in this way. That would provide a very promising lead, indeed, for, one then could try to control and increase the condition of the parent oysters kept in the laboratory in anticipation of the emission of larvae, by providing them with an ideal diet, included a given amount of flagellates to be used by the incubated larvae in more advanced stages of development. Under field conditions such larvae do already ingest tiny food particles according to the reviewer's personal experience.

Experiments on the removal of flagellates showed that at 20°C. a larva sweeps about 0·45 ml. clean of flagellates in 24 hours at a density of about 45 cells per mm^3. Larger larvae did not seem to remove more flagellates than

small larvae. It is not yet clear how under field conditions larval development may proceed very well at much lower concentrations of flagellates than those considered as optimal for the rearing under laboratory conditions. However, there is as yet no proof that the species of flagellates which have been tested in the laboratory form any significant part of the natural nanoplankton. As WALNE rightly remarks, there may be other species which are superior to those tested, but which do not thrive in the culture media used thus far. It could also be that a mixed diet as used in the field leads to better results than the feeding with a pure culture of one species only; but few experiments only have been carried out with carefully balanced diets consisting of more species.

WALNE is also worried about the fact that very often his larvae failed to swim continuously. Prolonged resting on the bottom of the jar often preceeds failures. He supposes that the metabolism is insufficiently rapid to permit continuous swimming, and that in the field they may in part rely on turbulence and the length of the water column to keep them afloat. The reviewer observed repeatedly that the larvae do often take a rest, falling down slowly, velum expanded, but resume swimming after having dropped over some 50 cm. In nature this will rarely bring them in contact with the bottom, but in the small jars such intermittent resting seems hardly possible without touching the bottom, where they may meet trouble.

It is interesting to note that salinity toleration is quite considerable. Good results were obtained from 26 to 35 $^0/_{00}$, but it is not recorded whether the parent oysters came from water with a high or a low average salinity, and with greater or smaller daily ranges in salinity.

P. Korringa

P. R. Walne. "The biology and distribution of the slipper limpet *Crepidula fornicata* in Essex rivers." Min. Agric., Fish and Food, Fish. Invest., Ser. 2, **20** (6): 1–50, 33 figs. London, 1956.

The investigations discussed in this paper were carried out to increase the knowledge on the biology of an important pest of the east coast oyster beds of England, a pest which is steadily extending its range, and is now found on nearly all the important oyster grounds on the English coast.

Conditions appealing to oysters correspond so very closely to those under which *Crepidula* thrives that it is virtually impossible to select oyster grounds which are ecologically unsuitable to the slipper limpet. The abundance of *Crepidula* even forms a very good guide to the hydrographic suitability of an area for oyster farming.

WALNE's studies elucidate many aspects of *Crepidula*'s biology, but do not bring much essential news on the true character of the damage inflicted to oyster farming, which can be summarized as: accumulation of mud, competition for food and space — very hard to put down in figures — and an increased laboriousness in oyster farming.

The conclusion that resistance to air frost is similar in *Mytilus edulis* and *Crepidula fornicata*, and is apparently correlated with the time taken for the tissues to freeze, should be considered with caution, as data obtained with sublittoral west coast mussels have been used. The reviewer's experience is that mussels living in the intertidal zone are much hardier to air frost than *Crepidula* living on beds exposed at low tide, though shell thickness may be about equal.

Very interesting are the observations on growth of *Crepidula* under natural conditions, a subject very difficult to study, as linear measurements do not always lead to trustworthy results. Size appeared to be no criterion of age in adult *Crepidula*, as growth is strongly modified by the limitation of the substratum. The oldest members in the chains are very often somewhat smaller than those in the middle of the chain, and side chains rarely yield individuals with fair-sized shells. This again is due to lack of substratum surface. As a result of restricted space side chain limpets are found to stop growth sooner or later, and apparently die speedily soon after. Migration to a more suitable substratum does not occur at a more advanced age. Even of the juveniles it could be induced that they must have metamorphosed close to, or even on, the clusters of adults.

Despite these difficulties WALNE could construct growth curves, and concludes that about one slipper limpet is added in the terminal position to a chain each year, and that individuals measuring 4 cm. are about 7 years old.

Comparative observations on the distribution of other larger epibenthic invertebrates are presented in an effort to forecast the extent to which *Crepidula fornicata* may become a pest if introduced elsewhere. The reviewer is, however, of opinion that the potential density of *Crepidula* populations can vary widely in areas which are hydrographically very similar, as the amount of suitable and durable substratum available per unit of surface may be very different.

Removal of such substratum, included empty shells and entire chains of *Crepidula*, efficiently done by power dredges, is in the long run the best method of control. It may be interesting to add to the description of the laborious methods to dispose of fished-up *Crepidula* that a cheap and tidy way is to dump them overboard in deep water with a bottom of coarse sand. Here they will be smothered within a very short time, provided tidal currents keep the sand perpetually in motion, and the empty shells will sink deeper and deeper in the sand and will never serve as a substratum again.

P. Korringa

Current Bibliography

Prepared by A. R. Margetts

Note. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the General Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indices.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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